Universidade Federal do Paraná

Setor de Ciências Biológicas

Programa de Pós-Graduação em Ecologia e Conservação

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PADRÕES MACROECOLÓGICOS DE DIVERSIDADE VEGETAL E PRIORIDADES DE CONSERVAÇÃO DA MATA ATLÂNTICA

Curitiba

2015

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Victor Pereira Zwiener

Tese apresentada ao Programa de Pós-Graduação em Ecologia e Conservação da Universidade Federal do Paraná como requisito parcial à obtenção do grau de Doutor em Ecologia e Conservação.
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Curitiba

2015

Ministério da Educação
UNIVERSIDADE FEDERAL DO PARANÁ
Setor de Ciências Biológicas
PROGRAMA DE PÓS-GRADUAÇÃO EM
ECOLOGIA E CONSERVAÇÃO

PARECER

Os abaixo-assinados, membros da banca examinadora da defesa da tese, a que se submeteu **Victor Pereira Zwiener** para fins de adquirir o título de Doutor em Ecologia e Conservação, são de parecer favorável à **APROVAÇÃO** do trabalho de conclusão do candidato.

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Dedico este trabalho aos meus pais, irmãos e a Déa

AGRADECIMENTOS

- À Márcia Marques e André Padial pelas oportunidades, paciência, discussões, confiança e liberdade para desenvolver a tese.

- Ao Townsend Peterson e Jorge Soberón pela orientação durante o doutorado sanduíche, pela parceria e ideias que contribuíram muito para minha formação.

- Ao Andrés Lira-Noriega, Narayani Barve, Vijay Barve, Lindsay P. Campbell, Jacob C. Cooper pela amizade e auxílio na preparação dos dados, programação, scripting e análises em geral.

- À Andrea Macedônio de Carvalho por ajudar na digitação dos trabalhos compilados, pela paciência e incentivo quando as energias e esperanças já estavam acabando.

- Ao laboratório de ecologia vegetal da UFPR (LEV) e todos os seus integrantes pela ajuda, amizade, disponiblidade de espaço físico e computadores.

- Ao Marcelo Tabarelli, André M. Amorim e seus estudantes e colaboradores por disponibilizar trabalhos de florística e fitossociologia.

- Ao Rafael Loyola e Frederico Faleiro pela parceria, sugestões e compartilhamento de dados.

- À CAPES pela concessão da bolsa de doutorado.

- Ao CNPq pela concessão da bolsa de doutorado sanduíche.

- Ao Programa de Pós-graduação em Ecologia e Conservação da UFPR pelo apoio logístico.

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RESUMO GERAL

Os organismos estão distribuídos em diferentes locais e por diferentes extensões geográficas gerando variação na estruturação espacial da biodiversidade. Essa variação é um dos padrões mais antigos e estudados em ecologia e biogeografia, no entanto muitos padrões ainda permanecem obscuros, particularmente nos trópicos onde pouco se sabe sobre os mecanismos que moldam a biodiversidade, restringindo a eficácia de planos de conservação. Esta tese teve como objetivo geral explorar padrões espaciais de diversidade de plantas lenhosas em larga escala e, com base em modelos de nicho ecológico, gerar simulações de planos de conservação da Mata Atlântica em diferentes cenários socioeconômicos e climáticos. O primeiro capítulo explora a estrutura espacial da riqueza e composição de espécies, testa diferentes hipóteses macroecológicas e avalia o efeito em larga escala de variáveis abióticas e de recursos. No segundo capítulo foram geradas simulações de manejo (proteção de remanescentes e restauração de áreas degradadas) em diferentes cenários socioeconômicos e climáticos visando maximizar a conservação da Mata Atlântica e minimizar custos e conflitos com atividades econômicas. O terceiro capítulo trata do efeito de mudanças climáticas em padrões de diversidade de plantas na Mata Atlântica, explorando os potenciais mecanismos e ameaças. O clima atual e fatores históricos e intrínsecos estruturados no espaço apresentaram grande importância na organização de metacomunidades. Dentre os fatores climáticos, variáveis representando energia e produtividade do ambiente e extremos de temperatura foram importantes preditores da riqueza e composição de espécies dando suporte à teoria energética e tolerância a fatores abióticos. Estes resultados salientam a importância de se investigar padrões de diversidade sob diferentes perspectivas e teorias a fim de se adquirir melhor entendimento dos mecanismos que promovem diversidade. O planejamento sistemático e ações de conservação envolvendo a proteção dos remanescentes e restauração de áreas degradadas são urgentemente necessários para minimizar a atual crise de biodiversidade e reduzir custos e conflitos com urbanização e atividades agropecuárias. Por fim alterações na estruturação de comunidades decorrente de respostas individualizadas de espécies frente a mudanças climáticas potencializam homogenização biótica no decorrer do tempo e ameaçam ainda mais a diversidade de plantas da Mata Atlântica.

ABTRACT

The organisms are distributed in different locations and geographical extents generating variation in the spatial structure of biodiversity. This variation is one of the oldest and most studied patterns in ecology and biogeography, however such patterns still remain unclear, particularly in the tropics where little is known about the mechanisms that shape biodiversity, limiting the effectiveness of conservation. This thesis aimed to explore spatial patterns of woody plant diversity on large scales and using ecological niche models, generate simulations of conservation plans for the Atlantic Forest in different socioeconomic and climate scenarios. The first chapter explores the spatial structure of species richness and composition, testing different macroecological hypotheses and evaluates the effects on large-scale of abiotic and resources variables. In the second chapter simulations were generated including protection of forest remnants and restoration of degraded land aimming to maximize conservation of the Atlantic Forest and minimize costs and conflicts with economic activities under different socioeconomic and climate scenarios. The third chapter assesses the effects of climate change on plant diversity patterns in the Atlantic Forest, exploring potential mechanisms and threats. The current climate and spatially structured historical and intrinsic factors had great importance in the organization of metacomunidades. Among the climatic factors, variables representing energy and productivity of the environment and temperature extremes were important predictors of species richness and composition supporting the energy and tolerance to abiotic factors theories. These results highlight the importance of investigating patterns of diversity from different perspectives and theories in order to gain a better understanding of the mechanisms that promote diversity. Systematic planning and conservation actions involving the protection of remnants and restoration of degraded lands are urgently needed to minimize the current biodiversity crisis and reduce costs and conflicts with urbanization and agricultural activities. Finally, changes in community structure arising from species individual responses to climate change enhance biotic homogenization over time and further threaten plant diversity in the Atlantic Forest.

1 INTRODUÇÃO GERAL

Padrões geográficos de diversidade têm sido descritos por mais de um século (WALLACE, 1878) e constituem um dos temas mais estudados em ecologia e biogeografia (CURRIE *et al*., 2004). Apesar de mais de 30 teorias e mecanismos terem sido sugeridos, muitos padrões ainda permanecem obscuros, particularmente nos trópicos onde a maior parte da biodiversidade está concentrada (WRIGHT, 2002; WILLIG *et al*., 2003). Além de importância teórica, o entendimento dos padrões e processos que promovem a biodiversidade é também de extrema importância para embasar políticas públicas que visam o uso eficiente de recursos e preservação do meio ambiente.

Os fatores que influenciam a distribuição de espécies e estruturação de populações e comunidades agem em diferentes escalas (MCGILL, 2010). Tradicionalmente estudos em ecologia optam por uma abordagem reducionista focando em experimentos em escala relativamente pequena de tempo e espaço com espécies mais acessíveis. Por conseguinte estes estudos avaliam principalmente fatores com maior influência em escala local e regional (ex: interações entre espécies, dinâmica e disponibilidade de recursos) e apesar de contribuírem para o avanço da área e fornecerem informações básicas essências para estudos em larga escala, pouco contribuem para a compreensão de mecanismos que atuam sobre grandes extensões geográficas (BROWN & MAUER, 1989; DINIZ-FILHO *et al*., 2009). Por outro lado a biogeografia histórica visa estudar processos agindo em larga escala de espaço e de tempo focando principalmente em processos evolutivos (CRISCI, 2001) e perde o detalhamento necessário para uma maior precisão. Com o crescente interesse de estudos ecológicos em fatores históricos e de larga escala, e de estudos biogeográficos e macroevolutivos em fatores regionais e contemporâneos, estas duas áreas têm experimentado um grande intercâmbio de ideias e teorias chegando à percepção de que o melhor entendimento dos padrões de diversidade é atingido considerando ambas as esferas de conhecimento (MORRONE, 1993; CRISCI, 2001; PETERSON *et al*., 2011).

O ambiente exerce grande influência na distribuição dos organismos (CAIN, 1971; WOODWARD, 1984). As variáveis ambientais podem ser classificadas de diversas maneiras, dependendo de suas relações e influências sobre a distribuição das espécies. Hutchinson (1978) foi um dos primeiros a perceber a necessidade de fazer distinções entre tais variáveis e propôs dividí-las em dois principais grupos: (i) variáveis cenopoéticas ou abióticas, que seriam variáveis que determinam as "condições gerais", não são consumíveis e portanto que não causam competição (ex. temperatura) e (ii) variáveis bionômicas ou bióticas que representam recursos consumíveis, que podem sofrer influência e gerar competição entre organismos (ex. nutrientes do solo). Austin e Smith (1989) e Austin (2002) propuseram uma classificação que distingue as variáveis em (i) diretas, que afetam organismos fisiológicamente e não são consumíveis (equivalentes às variáveis cenopoéticas), (ii) indiretas, que não tem efeito fisiológico causal, mas afetam organismos indiretamente através de variáveis correlatas (ex. altitude, latitude) e (iii) recursos, que seriam variáveis consumíveis e passíveis de competição (equivalentes às variáveis bionômicas). Essas classificações não são multuamente exclusivas, podendo uma certa variável exercer diferente influência sobre o organismos, dependendo do contexto e escala considerada (PETERSON *et al*., 2011). A compreensão dos mecanismos pelos quais o ambiente atua na distribuição de espécies é imprescindível para estabelecer uma síntese e fazer generalizações sobre padrões geográficos de biodiversidade.

No início do século XX Grinnell (1917) e Elton (1927) já atribuíam o conceito de nicho às regiões com condições ambientais (climáticas e de interações) adequadas para a ocorrência de determinadas espécies, mas foi Hutchinson (1957) quem atribuiu ao "nicho" à ideia de que seria um conjunto de características inerentes das espécies. Esta importante distinção possibilitou o estudo da distribuição das espécies em uma perspectiva individual, inclusive em contexto dinâmico no qual alterações ambientais podem modificar a distribuição das espécies (COLWELL & RANGEL, 2009; SOBERÓN & NAKAMURA, 2009). Hutchinson ainda fez a distinção entre nicho fundamental como sendo o conjunto de condições ambientais onde um determinado organismo pode potencialmente existir na ausência de competição, e nicho

realizado, como sendo condições ambientais onde o organismo ocorre devido a limitações impostas por interações com outros organismos. O reconhecimento do nicho como característica inerente das espécies também possibilitou uma maior integração entre ecologia e biogeografia histórica, pois nesta perspectiva o nicho também estaria sob influência de fatores históricos e passível de evolução (PETERSON *et al*., 1999; COLWELL & RANGEL, 2009; PETERSON, 2011). A formalização dos conceitos de nicho constitui uma das teorias mais influentes da atualidade, formando a base de muitos estudos teóricos e aplicados em ecologia e biogeografia.

A capacidade de dispersão é também um fator determinante da distribuição dos organismos e estruturação de comunidades (HUBBELL, 2001; SOBERÓN & PETERSON, 2005; LORTIE *et al*., 2004). Um exemplo disso é mostrado na Figura 1, considerando a distribuição do pinheiro do Paraná, *Araucaria angustifolia.* Considere a extensão geográfica ("G") da América do Sul, com ampla variação ambiental; os locais onde a espécie ocorre ("Go") é produto das condições ambientais apropriadas ou nicho fundamental ("A"), de interações com outras espécies ("B") e de sua capacidade de dispersão ou movimento ("M") que representa a região acessível à espécie em um período historicamente e ecologicamente relevante. Se considerarmos o espaço n-dimensional ou “espaço de nicho” (Fig. 1B) como sendo diferentes combinações de variáveis ambientais representadas por eixos de uma análise de componentes principais (PCA) é possível visualizar o conjunto de pontos, referente ao nicho realizado e pontos que representam regiões ambientalmente favoráveis além do alcance da espécie (“Gi”). Transferindo o conjunto de pontos para espaço geográfico é possível visualizar a localização das respectivas regiões (Fig. 1C). A Figura 1 também ilustra a incerteza envolvida em extrapolações, como as regiões indicadas climaticamente apropriadas para o pinheiro do Paraná na Amazônia, Bahia e sul da Patagônia. Isso ocorre porque não é possível estimar com precisão o nicho fundamental de espécies (“A”) com base em dados de ocorrência, devido à ausência de certas combinações ambientais dentro da área de dispersão (“M”), uma limitação já antecipada por Hutchinson, sendo necessários experimentação e estudos fisiológicos para obter estimativas precisas (PETERSON *et al*., 2011).

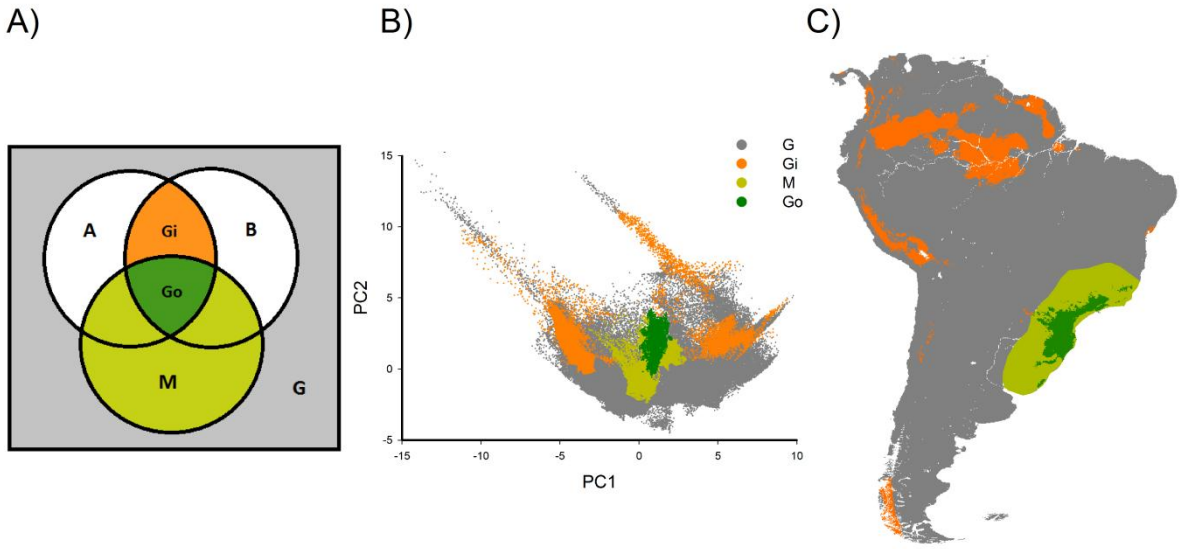

Figura 1. Representação esquemática da distribuição de espécies na América do Sul, tomando-se como exemplo a conífera *Araucaria angustifolia.* (A) diferentes fatores determinantes da ocorrência de espécies; (B) representação bidimensional do nicho ecológico de *Araucaria angustifolia*, e (C) respectivas regiões geográficas. A ocorrência (“Go”) é produto das condições ambientais apropriadas, ou nicho fundamental ("A"), de interações com outras espécies ("B") e de sua capacidade de dispersão ou movimento ("M"), áreas ambientalmente apropriadas também são estimadas além da capacidade de dispersão (“Gi”), porém com alta incerteza devido à dificuldade de estimar o nicho fundamental de espécies.

Padrões espaciais de diversidade podem ser gerados por fatores ambientais, biológicos e históricos estruturados no espaço. A estrutura espacial da diversidade pode ser vista como objeto de estudo ou como característica que compromete métodos estatísticos tradicionais e deve ser explicitamente considerada para testar hipóteses e avaliar a importância de diferentes fatores (LEGENDRE, 1993; DINIZ-FILHO *et al*., 2008). A constatação de que duas amostras retiradas em localidades geograficamente próximas são mais similares do que amostras distantes é conhecida como autocorrelação espacial. A ausência de independência estatística de observações obtidas ao longo do espaço geográfico é considerada uma forma de pseudoreplicação que aumenta a probabilidade de rejeitar a hipótese nula quando ela é verdadeira (LEGENDRE, 1993). A autocorrelação espacial não é considerada um problema quando as variáveis preditoras representam totalmente a estrutura espacial da variável resposta e quando processos intrínsecos que causam autocorrelação, como dispersão, são ausentes, nestes casos os resíduos não apresentam estrutura espacial (BEALE *et al*., 2010). No entanto ambas as

situações são virtualmente impossíveis em sistemas naturais, sendo necessários métodos apropriados para fazer inferências estatísticas.

A Mata Atlântica é um dos principais biomas brasileiros, ocorrendo ao longo da costa e em áreas florestais continentais do Rio Grande do Sul ao Rio Grande do Norte (STEHMANN *et al*., 2009). Devido à grande extensão geográfica, a Mata Atlântica possui ampla variação ambiental, como pluviosidade anual variando de aproximadamente 800 mm a 4.000 mm e temperaturas médias de 15 ^{o}C a 25 ^{o}C (IBGE, 1992; STEHMANN *et al*., 2009). Desta forma a Mata Atlântica apresenta condições ideais para o estudo de padrões espaciais de diversidade e fatores determinantes da riqueza e composição de espécies. A alta biodiversidade associada a elevados níveis de endemismo e impactos ambientais faz da Mata Atlântica um *hotspot* para conservação (MYERS *et al*., 2000). No entanto pouco se sabe sobre o potencial dos remanescentes na conservação da diversidade e praticamente nada se sabe sobre efeitos potenciais de mudanças climáticas na distribuição de espécies e estruturação de comunidades de plantas (COLOMBO & JOLY, 2010).

Esta tese teve como objetivo geral explorar padrões espaciais de diversidade de plantas lenhosas e, com base em modelos de nicho ecológico, gerar simulações de planos de conservação da Mata Atlântica em diferentes cenários socioeconômicos e climáticos. A tese está estruturada em três capítulos na forma de artigos escritos em inglês e formatados para submissão. O primeiro capítulo, já submetido e em fase de revisão na “Ecography”, explora a estrutura espacial da riqueza e composição de metacomunidades utilizando análises espaciais, testa diferentes hipóteses macroecológicas e avalia o efeito em larga escala de variáveis abióticas diretas e de recursos. No segundo capítulo, formatado para submissão na revista “Diversity and Distributions”, foram geradas simulações de manejo (proteção de remanescentes e restauração de áreas degradadas) em diferentes cenários socioeconômicos e climáticos visando maximizar a conservação da Mata Atlântica e minimizar custos e conflitos com atividades econômicas. O terceiro capítulo está formatado para a revista “Global Change Biology” e trata do efeito de mudanças climáticas em padrões de diversidade de plantas na Mata Atlântica,

explorando os potenciais mecanismos e ameaças impostas por alterações do clima.

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2 CAPÍTULO 1*

A importância relativa do nicho ambiental e processos de dispersão na estruturação de metacomunidades de plantas lenhosas em uma floresta tropical megadiversa

*Capítulo formatado de a cordo com as normas da revista científica *Ecography*

Unraveling the relative importance of environmental niche and dispersal processes in structuring woody plant metacommunities in a megadiverse tropical forest

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Understanding the causes for the geographic distribution of species and assembly of communities is one of the most intriguing questions in ecology and has become extremely important in face of global changes. This study aims to assess the broad-scale spatial structure of woody plant diversity, determine the importance of climatic relative to edaphic variables and of niche-related vs. dispersal/historical-related processes in structuring woody plant metacommunities. We compiled survey studies with abundance data (117 sites; 144,537 individuals) that sampled a minimum of 200 individuals with diameter at breast height ≥ 5cm in the Atlantic Forest. We selected climatic and soil variables that we hypothesized to have direct influence on plant growth. We constructed correlograms for species richness and composition and assessed the relative importance of predictors using spatially explicit generalized additive models (GAMs) coupled with information-theoretic analyses. Variation partitioning was used to infer the relative importance of niche-related vs. dispersal/historical-related processes. The spatial structure of species richness presented significant positive correlation of approximately ~ 435 km beyond which it became negative and again positive at the furthest distances, whereas compositional turnover showed positive correlation of ~ 690 km with decreasing similarity in increasing distances. Environmental variables related to energy/productivity and abiotic stress were important factors shaping richness patterns, with soil being less important at broad-scales. Species composition was significantly explained by both environmental and spatial variables. The spatial component showed similar amount of explanation compared to the environmental component. Our results suggest a combined contribution of environment, stochasticity, and historical processes as they represent important sources of variation in patterns of biodiversity. More importantly, a similar set of variables was good predictor of species richness and

composition, indicating a convergence of driving factors for both descriptors of plant communities.

Keywords

Tropical forest, energy theory, tolerance theory, metacommunity, climate, soil, generalized additive models, biodiversity, spatial structure, Atlantic Forest

A central issue in ecology and biogeography has been to understand the processes determining the species geographical distribution and assembly of biological communities (Gaston 2000, Willig et al. 2003). Questions about the key determinants of species richness, distribution, and co-existence have puzzled researchers for over a century (Wallace 1878, Rosenzweig 1995). Seeking to answer such questions has become increasingly important in order to predict and mitigate likely effects of global environmental changes on biodiversity and ecosystem functioning (Botkin et al. 2007, Bellard et al. 2012). While substantial theory on species distributions and diversity exists, a better validation from empirical studies is necessary for a more accurate understanding of the mechanisms that promote diversity (Gaston 2000, Currie et al. 2004).

Hypotheses to explain macroecological patterns of biodiversity can be broadly classified in two, non-mutually exclusive, classes with considerable evidence in the literature (Hubbell, 2001, Currie et al. 2004, Ricklefs 2004), here referred to as environmental-based and dispersal/historical-based hypotheses. Environmental-based hypotheses emphasize the influence of energy, seasonality, environmental heterogeneity, and abiotic stress on biodiversity and assembly mechanisms (Francis and Currie 2003); whereas dispersal/historical-based hypotheses focus on stochasticity, speciation, extinction and dispersal processes (Latham and Ricklefs 1993, Allen and

Gillooly 2006). Environmental and dispersal/historical processes act across different scales (Whittaker et al. 2001, Lortie et al. 2004) and generate spatial structure in diversity patterns which can be the sole focus of investigation or explicitly incorporated into analyses to precisely assess different biodiversity hypotheses (Legendre 1993, Peres-Neto and Legendre 2010, Beale et al. 2010).

Among environmental-based hypotheses, energy and tolerance to abiotic conditions have been depicted as important mechanisms at broad-scales (Hawkins et al. 2003, Currie et al. 2004). The basic idea of the energy hypothesis proposes that habitats under high energy inputs afford more individuals thus enabling larger populations and reducing extinction risk, which in turn, generates high regional and local species richness (Hutchinson 1959, Brown 1981, Wright 1983, Currie 1991). Tolerance to abiotic conditions states that the community in a particular area is composed only by species that can tolerate local conditions; species poor habitats tend to have mean conditions farther from physiological optimum with fewer species physiologically equipped to survive (Whittaker et al. 2001, Willig et al. 2003, Currie et al. 2004). Disentangling the relative importance of environmental drivers remains a current challenge for the understanding of biodiversity patterns.

The role of soil variables in structuring spatial patterns of plant diversity at broad-scales also remains unclear (Chave 2008). At local and regional scales, soil variables such as water availability, soil nutritional status and aluminum saturation, can strongly limit plant distribution (Sollins 1998). This occurs because species vary in their physiological tolerances and interespecific competition characteristics (Tilman 1982). Soil variables have less frequently been considered in broad-scale studies, particularly in the tropics, mostly due to scarcity of data (but see Marques et al. 2011, Ulrich et al. 2014).

74 The Atlantic Forest is a complex of ecosystems of great importance for the
75 maintenance of biodiversity and ecosystem services, originally extending over 1.5
76 million km^2 along the Brazilian coast and in continental areass (Stehmann et al. 2009).
77 Owing to its large geographical extent associated with elevations ranging from sea level
78 to 2,200 meters, the Atlantic Forest presents broad variation in climatic variables with
79 differences in annual mean rainfall ranging from about 800 mm to 4,000 mm and annual
80 mean temperature varying from 15 ^{o}C to 25 ^{o}C (Stehmann et al. 2009). Soil
81 characteristics also present considerable variation related to topography, type of bed-
82 rock and geological events (EMBRAPA 2013). Given the broad variation of
83 environmental variables and one of the highest levels of species richness and endemism
84 in the world (Myers et al. 2000), the Atlantic Forest represents an ideal system to assess
85 spatial structure and to compare the relative importance of different underlying driving
86 factors of plant diversity.

87 In this study we explore woody plant diversity patterns using the Atlantic Forest
88 as a study system. We directly compare environmental factors, which clearly have a
89 strong relationship with diversity gradients world-wide (Francis and Currie 2003,
90 Hawkins et al. 2003) and based on spatial analyses we infer about dispersal/historical
91 processes. More specifically, we expected a distance decay gradient of species richness
92 and turnover that would be mostly determine by variables related to energy, climatic
93 extremes (temperature and water availability) and dispersal/historical factors. We also
94 anticipated that edaphic variables would be less important than climate in structuring
95 woody plant metacommunities at broad-scales given that soil represents mostly
96 nutrients that species consume and compete for and thus its effect would be more
97 apparent at local scales.

98 **Material and methods**

99 **Data collection**

100 We compiled a dataset of 300 survey studies of natural forest remnants in the
101 Atlantic Forest (Supplementary material Appendix A1, Fig. 1). We searched for studies
102 in online academic databases, libraries of Brazilian universities and references cited in
103 the literature. We used the following terms to search online databases:
104 "phytosociology", "floristics", "forest", "structure", "trees", "woody plants" and
105 "Atlantic Forest". All potential studies were carefully inspected to exclude surveys that
106 considered only non-woody vegetation or were conducted in mangroves and shrubby
107 physiognomies. We made no restriction based on forest successional stage or
108 disturbance level. When two or more forests of different successional stages were
109 surveyed and only one geographical coordinate of the study site was provided, we
110 pooled the data for the locality. Conversely, if one study presented two or more surveys,
111 and provided distinct geographical coordinates for each site, information was extracted
112 separately for each survey. Finally, we only considered academic studies that were
113 published in scientific literature and/or passed through a peer review process (e.g.
114 completed Masters and PhD dissertation), reducing errors associated to species
115 misidentification and lack of scientific rigor. For each site, we compiled information of
116 species recorded, geographical coordinates and methods of data collection
117 (Supplementary material Appendix A1).

118 From each study we considered only species determined at the specific level.
119 The complete checklist was searched for spelling errors, incompatible homonyms,
120 varieties and unambiguous synonyms in the following electronic databases: "Lista de
121 Espécies da Flora do Brasil" (floradobrasil.jbrj.gov.br), the Tropicos (tropicos.org) and
122 The Plant List (theplantlist.org). We excluded approximately 10% of species after
123 quality control. Family classification followed APG III.

A common approach has been to analyze all compiled data without separating species according to data sampling method (Oliveria-Filho and Fontes 2000, Marques et al. 2011). This approach has the advantage of explaining general patterns but may compromise predictive power (Certain et al. 2014). We opted to construct a species x sites matrix containing the number of individuals of each species in each site for a subset of sites (117 sites; 144,537 individuals) that evaluated a minimum of 200 individuals with diameter at breast height (DBH) ≥ 5cm (Fig. 1), thus reducing variation associated to different sampling criteria.

Environmental variables

We selected climatic and soil variables that we hypothesized to have direct influence on plant growth and that are surrogates or control overall nutrient availability in soils. We opted not to include elevation as predictor, given it is an indirect variable representing effects correlated with other variables (e.g. temperature or rainfall) (Austin and Smith 1989, Austin 2002).

We obtained climatic data from the WorldClim database (http://www.worldclim.org; Hijmans et al. 2005), from which we chose seven bioclimatic variables: annual mean temperature (BIO1), mean diurnal range (BIO2), maximum temperature of warmest month (BIO5), minimum temperature of coldest month (BIO6), annual precipitation (BIO12), precipitation of wettest (BIO13) and driest months (BIO14). These variables represent annual trends and variability of climatic factors which govern growth rates and the maintenance of plant physiological integrity (Austin and Smith 1989, Hijmans et al. 2005). Soil variables were obtained from ISRIC – World Soil Information (http://www.isric.org; Batjes 2012). From this database we selected five quantitative soil variables which represent physical and chemical

properties of soils that may affect plant performance: exchangeable aluminum percentage (ALSA), effective cation exchange capacity (ECEC), soil pH measured in water (PHAQ), available water capacity (TAWC), and total organic carbon content (TOTC). Additionally, we obtained data of annual actual evapotranspiration (AET) from http://www.cgiar-csi.org (Trabucco and Zomer 2010). AET can be grossly defined as an estimate of the amount of water used to match the environmental energy demand or simply the amount of water actually lost by the vegetated surface (Whittaker et al. 2001). It thus estimates water-energy balance and is recognized as a good correlate of plant productivity and indicator of drought stress suffered by plants (Austin and Smith 1989, Willig et al. 2003). All variables were at spatial resolution of 5.0' (~10km at the equator) based on data accuracy. To avoid potentially misleading identification of relevant variables due to high collinearity, we constructed a correlation matrix (Pearson's correlation) and deleted variables with coefficient $|r| \geq 0.7$ (Dormann et al. 2013). We excluded BIO1, BIO12 and ECEC accordingly (Supplementary material Appendix A2).

Statistical analysis

Woody plant species richness was obtained by summing species occurrences in each site. Given that species richness obtained from field studies is likely a biased estimation due to different sampling efforts (Cowell et al. 2012, Supplementary material Appendix A3, A4), all richness analyses were based on estimates obtained from extrapolation of individual-based rarefaction curves (Supplementary material Appendix A4). The standardization procedure, implemented in the computer program Estimate S v.9.1 (http://viceroy.eeb.uconn.edu/estimates/), was applied only to richness and was not intended as means to compare different studies.

To assess and describe spatial structure of diversity we explored spatial autocorrelation of species richness and composition as a function of geographic distance. We constructed univariate correlograms based on Moran's *I* spatial correlation statistics for species richness and multivariate correlograms based on Mantel test of Jaccard's similarity matrices for species composition. Correlograms were generated as follows: (1) construction of a pairwise distance matrix based on geographical coordinates of sites; (2) delimitation of distance classes between sites; (3) Calculation of Moran's *I* and Mantel correlation coefficients for species richness and composition, respectivelly, at each distance class (see Sokal and Oden 1978; Bocard and Legendre 2012 for details). These spatial statistics measure resemblance of pairs of values or matrices located within predefined distance classes; for instance high values of Moran's *I* and Mantel correlation coefficients indicate that species richness and composition of sites are more similar within a distance classe than among classes. Spatial correlation may be significantly positive or negative when distance classes are more similar or dissimilar than randomly selected pairs (Legendre and Legendre 2012).

The number of distance classes of correlograms was defined according to Sturge's rule, significance was infered based on 10,000 permutations and sequential Bonferroni correction (Legendre and Legendre 2012). For better interpretation of correlograms, we show maps of species richness and compositional turn-over, represented by sites scores on the first axis of a non-metric multidimensional scaling ordination (NMDS). Alternatively, distance-decay in composition similarity was investigated by regressing pairwise community similarity against geographic distances (Appendix A6).

The fact that two samples taken from neighboring localities are more similar than distant samples is known as spatial autocorrelation (Sokal and Oden 1978,

Legendre 1993). The lack of statistical independence of observations obtained over geographical space is considered a form of pseudoreplication (Legendre 1993; Peres-Neto and Legendre 2010), which may affect hypothesis testing and model selection (Legendre 1993, Diniz-Filho et al. 2008). Spatial autocorrelation is not considered a problem when predictors fully represent the spatial structure of response variables and when intrinsic processes that cause autocorrelation, such as dispersal, are absent, in these cases model residuals do not exhibit spatial structure (Dormann 2007, Beale et al. 2010).

We used generalized additive modeling (GAM) coupled with model selection and multimodel inference to estimate the relative importance of climatic and soil variables driving species richness patterns. GAM is an extension of GLM framework allowing for non-linear response curves; it can be seen as a data- rather than model-driven approach (Hastie and Tibshirani 1990, Austin 2002). We used thin plate spline regression, simplified to a maximum of 4 degrees of freedom, to model the relationship of covariates, and included geographic coordinates with tensor product smooths to account for spatial structure of underlying driving factors (see Wood 2003, Dormann 2007, Beale et al. 2010 for mathematical explenations and R scripts). Tensor product smooths have the property of being invariant to rescaling of covariates and are appropriate to model spatial variation associated to unmeasured variables, given that unaccounted factors generating spatial structure may act in different scales and be measured in fundamentally different units (Wood 2006, Peres-Neto and Legendre 2010). Negative-binomial distribution with a log-link function was used for the error term.

The most parsimonious model and relative importance of environmental variables were obtained by comparing bias-corrected Akaike's information criterion

(AICc) of a set of candidate models and summing the Akaike's weights across all the models where a given variable occured (Burnham and Anderson 2002). We opted for an exploratory approach by generating all combinations of environmental variables and the intercept (null model) as candidate models, and inserted a spatial variable, represented by the tensor product smooths of geographic coordinates, as a fixed covariate reducing possible misleading variable selection due to spatial autocorrelation (Diniz-Filho et al. 2008).

We estimated the amount of variability of species composition explained solely by environmental and spatial components and also variability explained by spatially structured environmental variation using partial redundancy analyses (RDA). To explicitly account and estimate the spatial component structuring plant communities, we generated a series of spatial variables based on eigenfunction analyses, also known as spatial filtering, or Moran's eigenvector maps (Griffith and Peres-Neto 2006). This procedure was performed in the following steps: (1) construction of a pairwise distance matrix among communities based on geographical coordinates of sampling units; (2) construction of a weighted neighborhood matrix by truncating the distance matrix according to the maximum distance that connects all sampling units under minimum spanning tree criterion; (3) derivation of eigenvectors by principal coordinate analysis on the truncated weight matrix. The orthogonal eigenvectors are then used as spatial predictors (or spatial filters) and provide an objective way of assessing spatial structure at different scales (Borcard et al. 2004).

To estimate environmental and spatial components of community composition variation we used the previously described ten climate and soil variables as predictors, and performed a forward selection procedure proposed by Blanchet et al. (2008) to the spatial filters with positive eigenvalues, to ensure that spatial predictors in the final

247 model significantly explain variance in community composition. The significance of
248 different components was inferred with 10,000 permutations, and comparisons of the
249 amount of variation explained were based on adjusted fractions (Peres-Neto et al. 2006).
250 Abundance data were Hellinger-transformed prior to analysis to optimize relationships
251 with preditors over the ecological gradient (Legendre and Gallagher 2001).

252 To visualize the relative contribution of environmental variables in structuring
253 plant communites in different regions of the Atlantic Forest, we applied RDA and
254 constructed ordination diagrams by ploting site constraints (linear combinations of
255 environmental variables - LC scores) and scores for constraining environmental
256 variables (Legendre and Legendre 2012). The generated triplot was then divided into
257 four quarters, and sites were coded in geographic space according to each quarter of the
258 plot.

259 Eigenfunction spatial analyses were performed using SAM 4.0 (Rangel et al.
260 2010). Moran's *I*, Mantel correlograms, GAM models, tables of information criteria,
261 forward selection procedure, NMDS and RDA analyses were conducted with the R
262 statistical environment (The R Foundation for Statistical Computing, 2014) using the
263 'mgcv' (Wood 2011), 'bbmle' (Bolker 2014), 'vegan' (Oksanen et al. 2013) and 'letsR'
264 (Vilela and Villalobos 2015) packages. Variation partitioning with RDA were carried
265 out in VarCan software v.1 for Matlab (Peres-Neto et al. 2006).

266 **Results**

267 We recorded a total of 2,948 species in the complete dataset and a subset of
268 1,704 species with abundance data in surveys studies that evaluated only those
269 individuals with diameter at breast height ≥ 5cm in the Atlantic Forest. Estimated
270 species richness obtained from extrapolation/rarefaction of species accumulation curves

271 varied from 24 to 240 species. Richness peaked in the portion ranging from the southern
272 state of Bahia (BA) to the state of São Paulo (SP). Species accumulation curves did not
273 stabilize for the most species rich sites, suggesting that more species would have been
274 recorded with increasing sample effort (Supplementary material Appendix A5).

275 The spatial structure of species richness showed a patchy pattern with similar
276 number of species in sites located close to one another (positive correlation in short
277 distances of ~435 km) and at the extreme ends of the biome (positive correlation in long
278 distances of ~2600 km). Large differences in species richness were observed at
279 intermediate distances (negative correlation between distances of ~850 to ~2290 km)
280 (Fig. 2A). The spatial structure of species composition showed a gradient pattern with
281 similarity between sites decreasing with increasing distances (Fig. 2B, Appendix A6).
282 Composition of sites was positively correlated up to ~690 km (Fig. 2B).

283 The best model driving woody plant species richness comprised: actual
284 evapotranspiration (AET), minimum temperature of coldest month (BIO6) and soil
285 available water capacity (TAWC). Best candidate models showed low variability having
286 only three models with $\Delta AICc \leq 2$ and four predictor variables selected (i.e. AET,
287 BIO2, BIO6, TAWC). Model averaging results confirmed variables selected in the best
288 model of richness as the most important (Table 1). The best GAM model successfully
289 reproduced the spatial structure of observed richness and did not present significant
290 residual spatial autocorrelation. It presented a tendency to over-predict species poor
291 sites and under-predict species rich sites (Fig. 3).

292 Community composition was significantly explained by environmental and
293 spatial variables in partial RDA (Table 2). Communities in the northern region (lower
294 latitude) of the Atlantic Forest domain were positively correlated with extremes of

295 temperature (BIO5 and BIO6), whereas communities in the southern region (higher
296 latitude) were correlated with actual evapotranspiration (AET), temperature mean
297 diurnal range (BIO2), soil available water capacity (TAWC), soil exchangeable
298 aluminum percentage (ALSA) and precipitation of driest month (BIO14; Fig.4).

299 **Discussion**

300 Environmental similarity is expected to decline with increasing geographical
301 distance, making necessary to disentangle the relative roles of environmental filtering
302 and dispersal limitation to assess processes shaping diversity patterns over broad spatial
303 scales (Peres-Neto and Legendre 2010). Previous assessments of woody plant diversity
304 in the Atlantic Forest were mostly exploratory without explicitly addressing spatial
305 factors and macroecological hypotheses (Oliveira-Filho and Fontes 2000, Oliveira-Filho
306 et al. 2005, Marques et al. 2011). We found that species richness and composition are
307 spatially structured over large geographical extents, and that such patterns are affected
308 by current climatic conditions and dispersal related process. To our knowledge we
309 provide the first description of spatial patterns of woody plant diversity in the Atlantic
310 Forest based on a formal statistical framework, and assess the relative roles of dispersal
311 processes and environmental factors generating the observed patterns.

312 Contrary to classic latitudinal gradients in biodiversity, where lower latitudes
313 harbor the highest biodiversity (Gaston 2000), species richness was not higher in the
314 lowest latitudes at the studied scale. The observed patchy spatial pattern correspond to a
315 peak of richness in the mid costal region of the Atlantic Forest. Additionally,
316 community composition shows a gradient pattern with decreasing similarity in
317 increasing distances. Thus, the mid region may harbor species from the northern and
318 from the southern region. In fact, whereas the northern region of Atlantic Forest is

319 influced by Amazon and Caatinga floras, the southern is affected by Parana river floras
320 (Oliveria-Filho and Ratter 1995, SanMartín & Ronquist, 2004); as such the mid region
321 is strongly influenced by multiple biomes (Brazilian Savanna, Amazon, and Caatinga;
322 Thomas et al. 1998), possibly explaining the highest biodiversity. Taken together, both
323 spatial structure of richness and composition suggest that different regions of the
324 Atlantic Forest have experienced different environmental/historical constraints.

325 We can not discard that spatial patterns of diversity are affected by
326 anthropogenic disturbance. Indeed, the Atlantic Forest has been systematically altered
327 by human occupation over successive economic cycles and currently its original cover
328 remains mostly in small fragments and secondary forests (Ribeiro et al. 2009). Widely
329 distributed species tend to have high dispersal capacity and tolerate different
330 environmental conditions (Morin and Chuine 2006, Slatyer et al. 2013), which are
331 common traits to secondary forest species (Guariguata and Ostertag 2001). Hence, the
332 observed spatial patterns of species richness and composition may have been influenced
333 by the conservation status and successional stage of forests possibly reducing richness
334 estimates of highly degraded regions (Silva and Tabarelli 2000) and increasing
335 similarity between geographically distant sites. Even so, the mid-region of the Atlantic
336 Forest, haboring the highest species richness, is highly impacted, reforcing our
337 suspicion of the observed ecological patterns and likely mechanisms promoting
338 diversity.

339 A combination of variables representing energy/productivity (AET) and
340 tolerance to extremes of temperature and water (BIO2, BIO6, TAWC) were selected in
341 the top-ranked models to explain biodiversity patterns. The mechanisms for commonly
342 observed correlations of energy/productivity variables with richness patterns are not yet
343 clear and some ramifications have been proposed (see Evans et al. 2005 for a

344 comprehensive review). While minimum temperature of coldest month is clearly a
345 constraint to species distribution in places that experience freezing temperatures, we
346 have found that it may also constrain species in warm climates. This result indicates that
347 even in warm climates species optimum and richness patterns may be related to lower
348 bounds of temperature variation. Soil conditions affect diversity of tropical forests at
349 local scales (Sollins 1998, Martins et al. 2015), however, this influence seems to scale
350 up only for TAWC given that climatic variables were clearly more important. Our
351 results present evidence to energy and tolerance hypotheses and emphasize the
352 importance of different drivers and mechanisms affecting plant richness.

353 As extensively reported by previous studies, plant community structure was
354 significantly explained by environmental and spatial constrains, suggesting a combined
355 contribution of environmental determinism, stochasticity and historical processes (e.g.
356 Tuomisto et al. 2003, Chave 2008). A long debate in the literature has been devoted to
357 discussing the relative role of environmental and spatial processes operating at multiple
358 scales to shape local community composition in the metacommunity framework
359 (Leibold et al. 2004; Chase 2005, Tuomisto and Ruokolainen 2008 and references
360 therein). Four metacommunity paradigms were proposed (Leibold et al. 2004): *species*
361 *sorting* - species do not experience dispersal limitation and are sorted only according to
362 environmental filtering; *mass effects* - species respond to environmental filtering, but
363 intense dispersal may overcome species exclusion in unsuitable habitats; *patch*
364 *dynamics* - good dispersers dominate isolated or recently disturbed communities, while
365 better competitors drive them to extinction in less-isolated or mature communities;
366 *neutral dynamic* - stochasticity in speciation, extinction and dispersal determine the
367 community structure (see review in Heino et al. 2015). These four paradigms can be
368 summarized into non-mutually exclusive general mechanisms: niche-related and

neutral-related (Heino et al. 2015). Niche-related mechanisms are considered the primary drivers, if community composition is mainly predicted by environmental variables (Cottenie 2005). On the other hand, a pure effect of spatial variables used here is usually interpreted as representing stochastic processes, including stochastic dispersal limitation and ecological drift (Cottenie 2005). In line with most studies, we argue that plant communities in the Atlantic Forest would not be structured by a single metacommunity paradigm, instead by a combination of environmental and dispersal/historical processes as they represent important sources of variation in patterns of biodiversity.

More importantly, our results provide interesting insights about the role of environmental determinism in plant communities. A similar set of environmental variables were good predictors of both species composition and species richness, indicating a convergence of environmental driving factors for both descriptors of plant communities. More than highlighting the importance of environmental determinism for plant communities, we also advocate that studies should dig further on environmental descriptors. Classic BioClim variables have been proved to be important predictors of biodiversity (Waltari et al. 2014), but soil variables, although playing a secondary role at broad-scales, seems also to be central for plant communities (see also Ulrich et al. 2014).

The data analyzed in this study are samples of local communities composed of species that have been able to reach and adapt to local biotic and environmental conditions. On the one hand, this type of data has the advantage that is resultant of multiple ecological and evolutionary mechanisms acting at multiple spatial and temporal scales (Lortie et al. 2004). On the other hand, field samples contain much variation related to local factors and correlations with broad-scale explanatory variables

may be weakened (Whittaker et al. 2001). Alternatively, one could stack species range maps (e.g. obtained from ecological niche modeling) and explore correlations with different drivers (Thuiller et al. 2006). This approach has been shown to result in stronger correlations but has a major drawback that it does not explicitly consider any rules based on ecological sorting that control species co-occurrences and may overestimate the total number and composition of species in a given site (Dubuis et al. 2011, Guisan and Rahbek 2011, but see Calabrese et al. 2014, Distler et al. 2015). Our approach contributes for predicting broad-scale patterns of plant assemblages and represents an important step towards understanding the factors that generate and constrain diversity in tropical forests.

The identification of spatial patterns may ultimately assist the formulation and testing of ecological hypotheses (Legendre & Legendre 2012). Indeed, here we identified spatial patterns and further investigated if climatic and edaphic variables may explain such patterns. We found empirical evidence of multiple driving factors, but, as expected, great amount of variation is not explained by environmental variables, suggesting combined contribution of niche and dispersal/historical processes in structuring woody plant metacommunities. Future research should aim at integrating niche-related and dispersal/historical-related processes for explaining and predicting current patterns of species assemblages. We innovated by suggesting that a similar set of climatic and edaphic variables explains both individual (species composition) and collective properties (richness) of woody plant metacomunities, contributing to the understanding of mechanisms that promote diversity in tropical forests.

Acknowledgments – We are thankful for the comments of Lindsay P. Campbell, Jacob C. Cooper, Marcelo Tabarelli and Jean Paul Metzger which greatly improved earlier versions of the manuscript. We would also like to thank Marcelo Tabarelli, André M.

Amorim and their crew for providing access to papers and checklists. The Brazilian Research Council (CNPq) provided grants to MCMM (Grants 304650-2012-9 and 229349-2013-7) and the Brazilian Education Council (CAPES) provided scholarship to VPZ.

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Table 1. General Aditive Models (GAM) driving species richness of woody plants for compiled survey studies in the Atlantic Forest of Brazil. Only variation of Akaike Information Criterium (ΔAICc) ≤ 2 is shown. At the bottom, multi-model inference showing the importance of each predictor variable (sum of AIC weights across GAM models with a given variable). The three most important variables are highlighted in bold.

Predictor variables	AICc	df	ΔAICc	Weight	R^2 (adj)
AET + BIO6 + TAWC	1123.45	19.56	0.00	0.09	0.60
AET + BIO2 + BIO6 + TAWC	1124.83	20.35	1.37	0.05	0.61
AET + BIO6	1124.99	17.42	1.53	0.04	0.58

Multi-model inference: **AET=0.74**; BIO2=0.30; BIO5=0.20; **BIO6=0.93**; BIO13=0.18; BIO14=0.18; ALSA=0.20; PHAQ=0.18; **TAWC=0.54**; TOTC=0.21.

AET=actual evapotranspiration; ALSA=exchangeable aluminum percentage; BIO5= maximum temperature of warmest month; BIO6= minimum temperature of coldest month; BIO13=precipitation of wettest month; BIO14=precipitation of driest month, PHAQ=soil pH, TAWC=soil available water capacity; TOTC=total organic carbon content

Table 2. Variation partitioning of community composition with Redundancy Analysis (RDA) in relation to environment (climate and soil) and space (filters). The components [A] and [C] represent variance explained by pure environmental and spatial factors, respectively, whereas component [B] represents variance explained by spatially structured environmental variation.

Effects	R^2(adj)	*P*
[A+B+C]	0.22	0.001
[A+B]	0.14	0.001
[C+B]	0.17	0.001
[A]	0.06	0.001
[B]	0.08	-
[C]	0.08	0.001
[A] vs. [C]	-	0.040
Residual	0.78	-

Figure legends

Figure 1. Location of compiled plant survey studies that evaluated individuals with diameter at breast height ≥ 5cm in the Atlantic Forest. Brazilian states: Rio Grande do Sul (RS); Santa Catarina (SC); Paraná (PR); São Paulo (SP); Mato Grosso do Sul (MS); Goiás (GO); Rio de Janeiro (RJ); Espírito Santo (ES); Minas Gerais (MG); Bahia (BA); Sergipe (SE); Alagoas (AL); Pernambuco (PE); Paraíba (PB); Rio Grande do Norte (RN).

Figure 2. Moran's I correlogram and map of rarefied richness (A); Mantel correlogram and map of species composition turnover (B). Empty symbols indicate lack of spatial autocorrelation; filled symbols above the dashed line correspond to positive autocorrelation and below to negative autocorrelation, tested with 10,000 permutations. Map symbols are proportionally scaled to richness values (A) and colored according to values of the first axis of a two-dimensional NMDS ordination (STRESS=20) based on Bray-Curtis dissimilarity (B). Similar colors indicate similar composition. Richness and score values of the NMDS are categorized according to ten natural-breaks (Jenks algorithm).

Figure 3. Linear regression of observed vs. predicted richness from the best selected General Aditive Model (GAM) (A) and Moran's I correlogram (B) of predicted richness (circles) and model residuals (triangles). Points above the dashed line in 'A' correspond to over-prediction and below to under-prediction. Empty correlogram symbols indicate lack of spatial correlation; filled symbols above the dashed line correspond to positive correlation and below to negative correlation, tested with 10,000 permutations.

Figure 4. Redundancy analysis (RDA) triplot of the species composition data constrained by environmental variables, and location of compiled plant survey studies coded in geographic space according to each quarter of the plot.

Fig1.

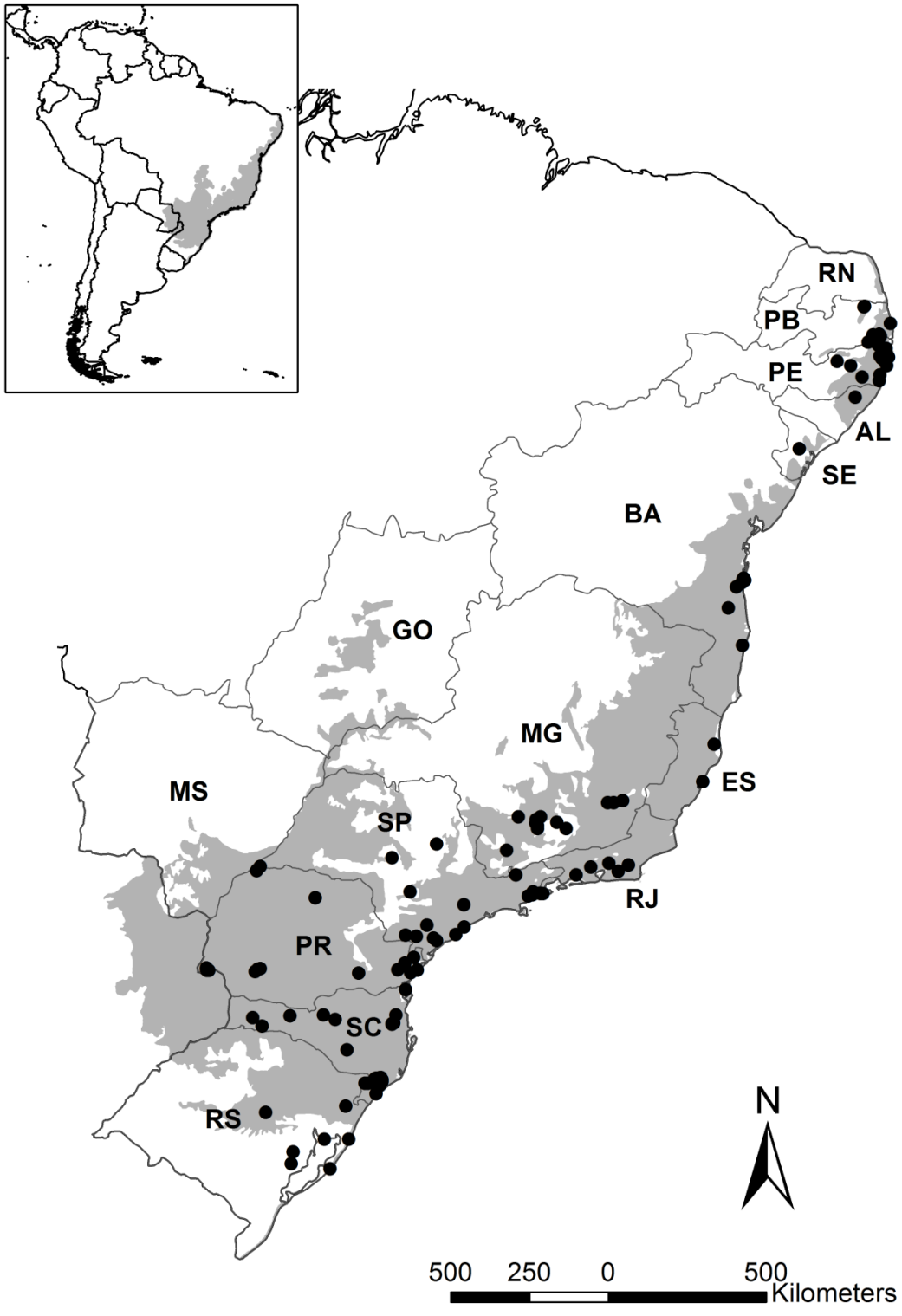

RN
PB
PE
AL
SE
BA
GO
MG
ES
MS
SP
RJ
PR
SC
RS
N
500 250 0 500
Kilometers

Fig. 2

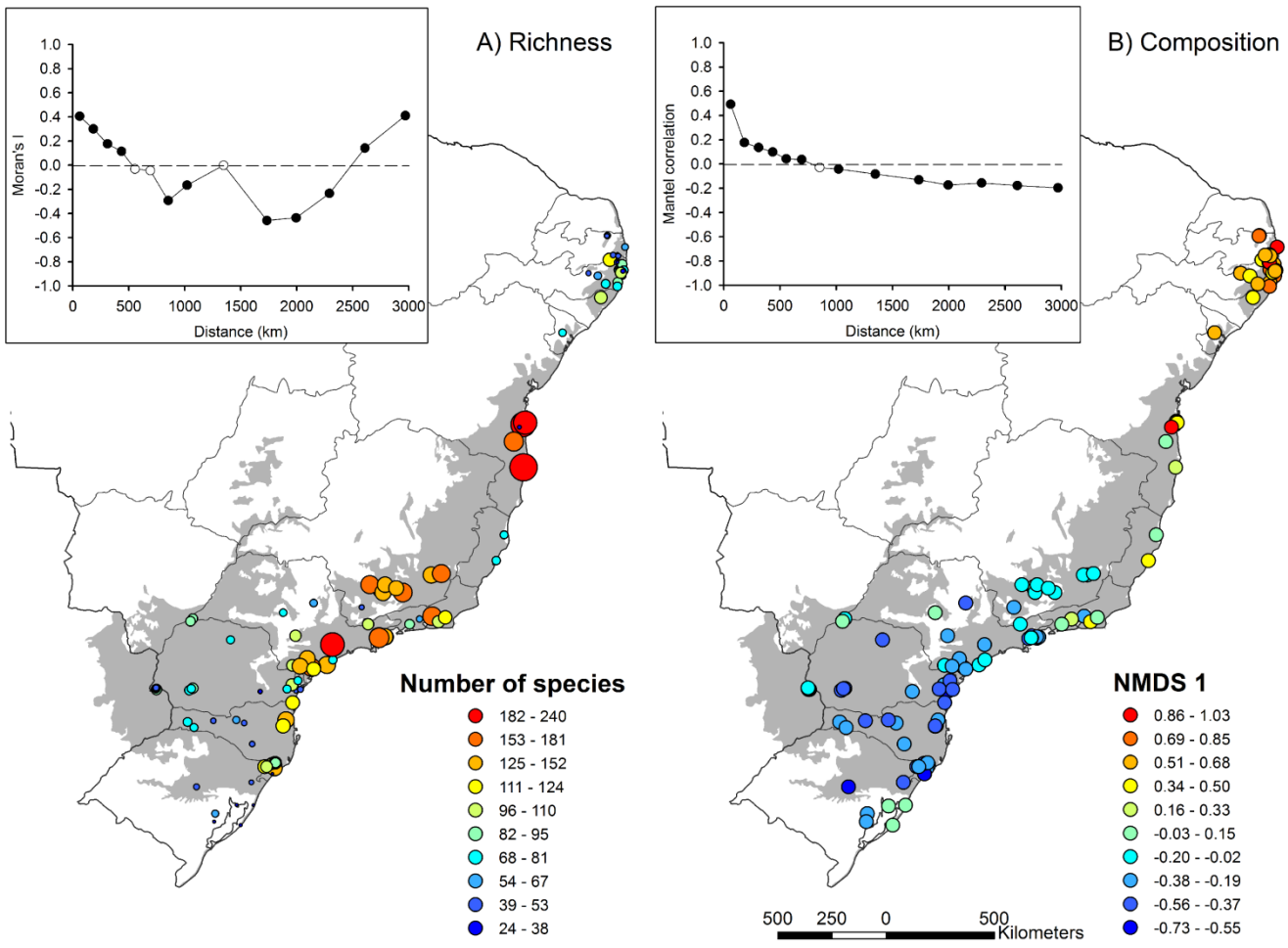

A) Richness
Moran's I
Distance (km)
B) Composition
Mantel correlation
Distance (km)
Number of species
182 - 240
153 - 181
125 - 152
111 - 124
96 - 110
82 - 95
68 - 81
54 - 67
39 - 53
24 - 38
NMDS 1
0.86 - 1.03
0.69 - 0.85
0.51 - 0.68
0.34 - 0.50
0.16 - 0.33
-0.03 - 0.15
-0.20 - -0.02
-0.38 - -0.19
-0.56 - -0.37
-0.73 - -0.55
500 250 0 500
Kilometers

Fig. 3

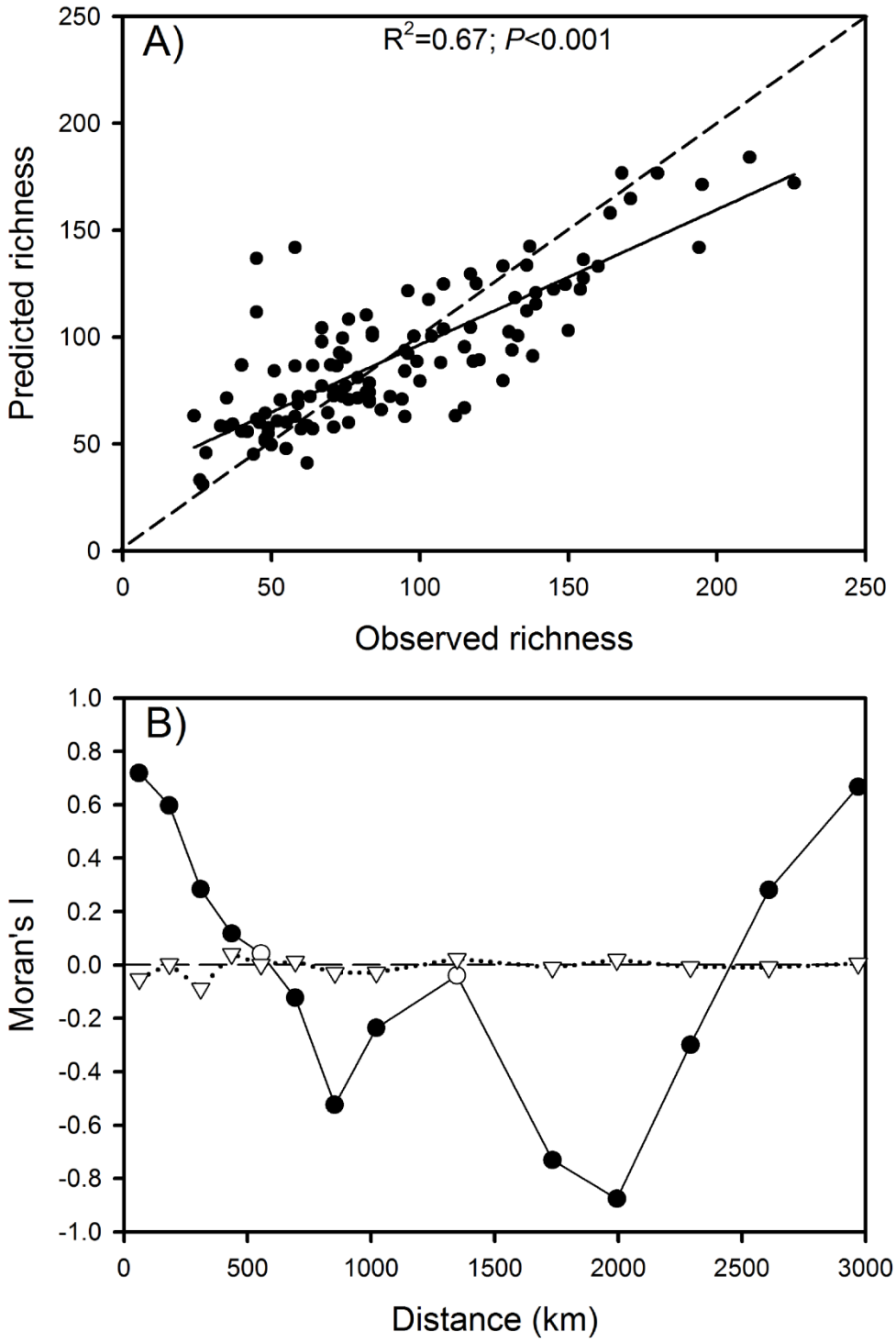
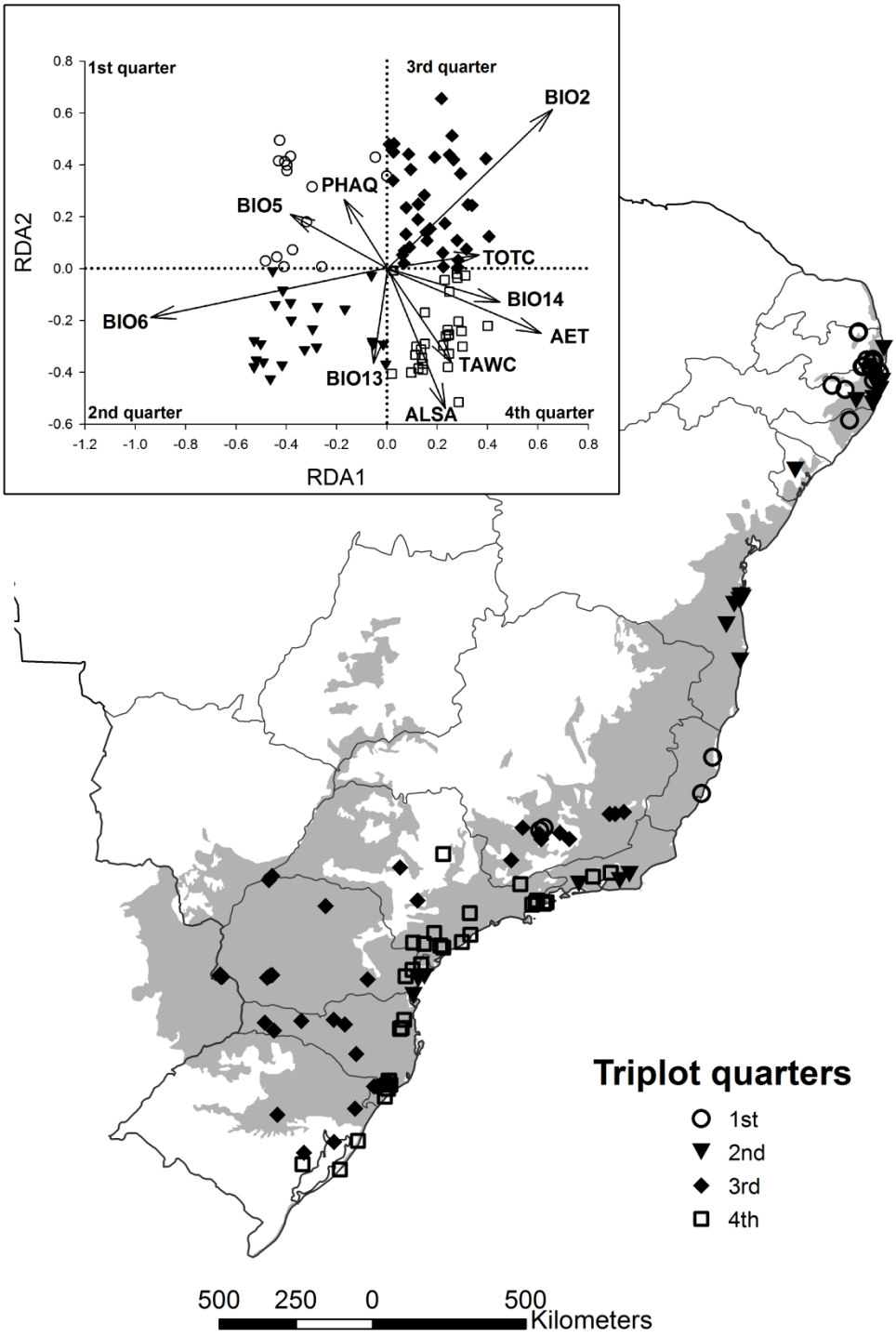

A)
R^2=0.67; *P*<0.001
Predicted richness
Observed richness
0
50
100
150
200
250
B)
Moran's I
Distance (km)
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
0
500
1000
1500
2000
2500
3000

Fig. 4


1st quarter
3rd quarter
2nd quarter
4th quarter
BIO2
PHAQ
BIO5
TOTC
BIO14
BIO6
AET
TAWC
BIO13
ALSA
RDA1
RDA2
Triplot quarters
1st
2nd
3rd
4th
500 250 0 500
Kilometers

3 CAPÍTULO 2

Prioridades para conservação e restauração da Mata Atlântica em face à mudança climática

*Capítulo formatado de acordo com as normas da revista científica *Diversity and Distributions*

On the urgent need for conservation and restoration planning: the case of climate and land-use changes in the Brazilian Atlantic Forest

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Running title: Conservation priorities in the Atlantic Forest

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ABSTRACT

Aim. To propose and compare priority sites for conservation and restoration of woody plants under diverse climate and land-use scenarios, considering socioeconomic costs, presence of protected areas, and distribution of forest remnants.

Location. The Atlantic Forest Biodiversity Hotspot, Brazil.

Methods. We used ecological niche modeling to estimate potential distributions for 2255 species under current and contrasting future climate change scenarios. We obtained spatially explicit land-use projections, maps of forest remnants derived from remote sensing, and socioeconomic variables for each municipality within the Atlantic Forest region. We used niche models, land-use data and socioeconomic data to assess spatial priorities that complement the current network of protected areas under different management scenarios: (1) conservation of forest remnants only; (2) conservation of remnants followed by restoration of degraded habitat; and (3) unconstrained actions, in which management direction is not defined *a priori*. We compared our results under different levels of land protection, with targets of 10, 17 and 20% of the Atlantic Forest.

Results. Present forest remnants covered only 12% of the Atlantic Forest, so targets of 17% and 20% can be achieved only via active restoration. Targets of 17% and 20% captured most species, and represented on average 26-34% of species' distributions. The spatial pattern of degraded habitats negatively affected representation of biodiversity and implied higher costs and reduced efficiency. No difference was observed between conservation prioritizations based on contrasting climate change scenarios.

Main conclusions. Protection of forest remnants alone will not be sufficient to safeguard woody plant species under climate and land-use changes; therefore, restoration actions are urgently needed. With integrated management actions and multi-criterion nationwide planning, reaching the 17% Aichi biodiversity target will constitute an important step towards protecting Atlantic Forest biodiversity.

Keywords

Systematic conservation planning; climate change; land use change; ecological restoration; conservation targets; ecological niche modeling

INTRODUCTION

Tropical forests play crucial roles in maintenance of global biodiversity and regulation of ecosystem services (MEA, 2005; Gardner *et al*., 2009; Cardinale *et al*., 2012). Although vastly important for society, tropical forests are among the most threatened ecosystems in the world owing mostly to deforestation and habitat fragmentation caused by human activity (Brooks et al., 2002; Wright, 2005). Climate change also constitutes an eminent threat to biodiversity; in synergy with land-use changes, it may increase the extinction risk for many species (Brooks et al. 2008). Effective management actions accounting for both future climate and land-use changes are thus needed to mitigate effects of global environmental change (Thuiller et al. 2008; Araújo *et al*., 2011; Bellard *et al*., 2012; Faleiro *et al*., 2013).

Species may respond to climate change by acclimatization, evolutionary adaptation, and/or migration to more suitable areas. Although controversial, tropical plants are likely to have low acclimation ability because they are adapted to limited geographic and seasonal variation in temperature (Wright *et al*., 2009; Corlett, 2011; Feeley *et al*., 2012). Moreover, evolutionary adaptation and migration to suitable areas are unlikely to buffer effects of climate change, given that long generation times constrain evolutionary rescue, and movement will be reduced by immobile edaphic factors, interspecific competition, forest fragmentation, and loss of dispersal agents (Corlett, 2009; Price & Kirkpatrick, 2009). While some species with narrow environmental requirements will likely retract to "climate refugia" within their current ranges, others may go extinct (Thomas *et al*., 2004; Keppel *et al*., 2012; Gavin *et al*., 2014). Thus, assessing the effectiveness of current networks of protected areas for conservation of biodiversity under climate change, establishing new protected areas in climatically suitable areas, and restoring degraded habitats constitute important steps

towards reversing biodiversity declines (Hannah *et al*., 2007; Williams *et al*., 2008; Thomson *et al*., 2009; Araújo *et al*., 2011).

Many challenges involve effective conservation and management of biodiversity. In particular, knowing what fraction and which specific portions of the landscape need conservation intervention and management action is crucial to achieve proper conservation objectives (Margules & Pressey, 2000; Brooks *et al*., 2006; Wilson *et al*., 2007). From the perspective of biodiversity conservation, distributions of species are the basic information required. Ecological niche modeling has emerged as an important tool by which to assess species' current and future potential distributions, allowing for a dynamic conservation approach necessary to cope with climate change (Araújo & Peterson, 2012). Detailed data on other factors (benefits and costs) must be included in a multi-criterion framework to improve chances of successful management, such as presence of remnant natural habitat and existing protected areas, land-use type and changes, economic or opportunity costs, and political governance (Margules & Pressey, 2000; Pressey & Cowling, 2001; O'Connor *et al*., 2003; Faleiro & Loyola, 2013).

Addressing all species, communities, or ecological systems for conservation is highly impractical and costly, making necessary identification of clear conservation goals on which to focus planning and management efforts (Margules & Pressey, 2000). Systematic conservation planning techniques aim to make the best use of available resources to identify priority sites for management, based on principles such as comprehensiveness, adequacy, complementarity, and efficiency, in a quantitative, repeatable and transparent way (Margules & Pressey, 2000; Wilson *et al*., 2009). Planning for conservation of remaining habitat and restoration of degraded land differ essentially in that the latter considers locations that do not provide suitable habitat, but

could potentially given sufficient time and management effort (Noss *et al*., 2009; Thomson *et al*., 2009). The extent to which different management actions contribute to biodiversity conservation is largely unexplored, and constitutes an important topic of research for the formulation of sound conservation policies (but see Wilson *et al*., 2007; Possingham *et al*., 2015).

The Atlantic Forest is a complex of ecosystems of great importance for the maintenance of biodiversity, originally extending over 1.5 million km^2 along the Brazilian coast and in interior (Stehmann *et al*., 2009). The Atlantic Forest is considered a biodiversity hotspot, being one of the world's most species-rich biomes, with both high levels of endemism and high threat to its integrity (Myers *et al*., 2000; Mittermeier *et al*., 2011), yet little is known about the potential of forest remnants to conserve its diversity and functions. Given intense deforestation and anthropogenic disturbance, only a small portion of the original Atlantic Forest cover still remains; the remnants are distributed mostly in small fragments (Ribeiro *et al*., 2009).

Here, we apply ecological niche modeling coupled with systematic conservation planning, to assess and identify priority sites for conservation and restoration of woody plant species under contrasting climatic and socioeconomic future scenarios. We focus on the Atlantic Forest of Brazil in view of its high levels of plant diversity and endemism, and threats from human modification of landscapes. More specifically, we explore the following questions: (i) Is the current network of protected areas in the Atlantic Forest sufficient to protect woody plant species in face of climate change? (ii) How can different management actions complement the current protected areas for protection of biodiversity? (iii) How would different management actions affect representation of biodiversity?

METHODS

Focal species and occurrence records

The focal species were selected from compiled checklists of 300 field inventories, comprising 2948 woody plant species distributed across the extent of the Atlantic Forest. Occurrence records were obtained for each species from the field inventories, plus georeferenced data associated with herbarium specimens retrieved from speciesLink (http://splink.cria.org.br/) an electronic database of Brazilian primary biodiversity data currently containing over five million georeferenced records from 377 herbaria and natural history museums.

We removed duplicate records from the same locality, compared the geographic location of occurrences with range limits established by specialists (ranges from floradobrasil.jbrj.gov.br), and removed isolated records falling outside the species' natural range. We rarefied records from the same species so that no pairs of points were closer than 20 km; all other records were excluded to reduce effects of sampling bias and spatial autocorrelation on model performance (Hijmans, 2012; Boria *et al*., 2014). Hence, from a total of 673,096 geo-referenced records for 2948 species, we retained 286,798 records. We further considered species ≥15 independent records, which reduced the number of plant species to 2255 documented by 283,287 records.

Environmental variables and climate change scenarios

We obtained environmental variables for current and future climate projections from the WorldClim database (http://www.worldclim.org; Hijmans *et al*., 2005) at a spatial resolution of 5'. Future climate projections were based on the IPCC Fifth Assessment Report, from which we selected three general circulation models (CCSM4, GISS-E2-R, and MIROC5) from two representative concentrations pathways (RCP2.6

and RCP8.5) for the year 2050 (average for 2041-2060) and 2070 (average for 2061-2080). RCPs are baseline greenhouse gas emissions scenarios used as inputs to global climate models for future climate projections. RCP2.6 and RCP8.5 project low and high greenhouse gas emissions, and are associated with low and high intensity of climatic change, respectively (IPCC, 2013).

To reduce dimensionality and colinearity of environmental layers we conducted a principal component analysis (PCA) based on a correlation matrix of standardized variables. PCA was done with all current 19 'bioclimatic' variables and the values predicted to future climate projections. To characterize present and future environmental variation across the study region, we used the first six principal components, which accounted for >95% of overall variation in climatic variables.

Ecological Niche Models

We used ecological niche models (ENMs) as surrogates of species' potential distributions based on climatic suitability. Niche modeling has been used to estimate distributions in space and time, and represents an important tool in biodiversity conservation planning (Elith & Leathwick, 2009; Araújo & Peterson, 2012; Guisan *et al*., 2013).

One important decision in the process of building ENMs is definition of the accessible area used for calibrating the models (Barve *et al*., 2011). Ideally, this area should reflect the geographic region accessible to species in a relevant (ecologically and historically) amount of time (Peterson e*t al*., 2011; Barve *et al*., 2011). Here, we have approximated the accessible area for each species by plotting occurrence points on base maps, comparing the distribution of points to ecoregions (Olson *et al*., 2001), historical climatic stable areas in the Atlantic Forest (Fig.2 from Carnaval & Moritz, 2008), and

range limits of the species established by specialists (floradobrasil.jbrj.gov.br). These accessible areas ranged from the entire tropical and subtropical region east of the Andes, for widely distributed species, to restricted areas of the Atlantic Forest for narrowly distributed endemic species.

Several methods for estimating species niches' and related potential geographic distributions have been developed and explored (Peterson *et al*., 2011). We chose the maximum entropy, 'Maxent', method (Phillips *et al*., 2006), given its high prediction ability for small samples and adequacy with presence-only data (Wisz *et al*., 2008; Elith & Graham, 2009; Elith *et al*., 2010). We used the R package dismo (Hijmans *et al*., 2012) to build niche models, settings used were 5 bootstrap replicates, raw output, and a least training presence threshold over the median estimate to produce binary predictions while admitting $E = 5\%$ omission 'error' (Peterson *et al*., 2011; Merow *et al*., 2013). Other settings were kept as default.

The final ENMs prediction of each species, projected to each different time periods, climate model and emissions scenario, was compared in detail. Synthesis was obtained by overlaying thresholded projections from global climate models within the same RCP, and considering areas in which all three estimates coincided. Hence, we used a conservative estimate of potential distributions in the future.

Land use change scenarios

We obtained spatially explicit data on areas anticipated as urban, cropland, and pasture at present and forecasted for 2050 and 2070, from Land Use Harmonization (http://luh.umd.edu/). The data are provided as fraction of grid cell covered by each land-use category for different socioeconomic trends, and constitute an important

component in calculation of RCPs (Hurtt *et al*., 2011). We used projections from the IMAGE and MESSAGE models that link to RCP 2.6 and RCP 8.5, respectively.

Land cost and political willingness to act

For each of the 3096 municipalities within the Atlantic Forest extent, we obtained data on gross domestic product (GDP) in 2010 (http://www.ibge.gov.br). Based on municipal financial information (http://www.stn.fazenda.gov.br), we calculated average (2004–2010) percentage of GDP invested in environmental programmes. Total municipal GDP and percentage invested in environmental programmes were used as proxies for land cost and political 'willingness to act', respectively (see Balmford *et al*., 2003; Faleiro & Loyola, 2013).

Forest remnants and protected areas

We estimated the amount of forest remaining, based on Atlantic Forest fragments maps for 2012 (available at http://mapas.sosma.org.br/), a product of collaborative work that constitutes the most comprehensive survey of Atlantic Forest remnants (SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais, 2013). The current network of protected areas was retrieved from the Brazilian Ministry of Environment database (http://mapas.mma.gov.br/i3geo/datadownload.htm). We considered only strict protected areas (called "conservation units of integral protection" according to Brazilian environmental law) with a minimum size of 1000 ha, and discarded other smaller areas of less effective types of protection (called "conservation units of sustainable use").

Systematic conservation planning

We used the Zonation framework and software (v.4.0; Moilanen *et al*., 2009) to rank sites and obtain spatial priorities for conservation of woody plant species in the Atlantic Forest. Prioritizations were performed aiming at reducing socioeconomic conflicts (with urbanization, agriculture, and livestock) and costs (land cost), while maximizing political willingness to act, and accounting for effects of land-use and climate change on species' distribution. Zonation applies a reverse heuristic algorithm which starts from the full planning region and iteratively removes sites (pixels or grid cells) from least to most important according to distribution of features (species' distributions, land-use, land cost, and political willingness), assigned weights, and connectivity, producing a nested hierarchic ranking of conservation priorities for all cells across the planning region (hereafter termed a "prioritization solution").

We set the additive benefit function (ABF) as the cell removal rule. The ABF favors grid cells with higher species richness and accounts for complementarity (i.e., sites are selected to complement one other in the features they contain). The ABF is indicated when species are essentially surrogates or samples from a larger regional species pool, resulting in a priority ranking that on average has a high performance, but may retain a low minimum proportion of original distributions for the worst-off species (Moilanen, 2007; Moilanen *et al*., 2009; Moilanen *et al*., 2012 for details).

Trade-offs between biodiversity, socioeconomic, land cost, and political features were defined by assigning positive weights to beneficial factors (features that should be maximized to increase conservation effectiveness and opportunity) and negative weights to constraint factors (features that should be minimized to avoid conservation conflicts). We assigned equal weights to each species at +1/1683 (1/highest richness) and political willingness to act at +0.2, whereas land cost, forecasted urbanization, cropland, and pasture area were each weighted at -0.3. The sum of positive and negative

weighted features was thus 1, allowing a balanced solution in the prioritization (Moilanen *et al*., 2011; Faleiro & Loyola, 2013).

Zonation also allows use of positive interactions within species from one site to another or from one time step to another (Carroll *et al*., 2010). Hence, we accounted for effects of climate change by adding interactions (connectivity) between species' present distributions and future projections, making a conservative assumption of no dispersal, in which species' ranges can only retract but not expand or colonize.

We sought to identify priority areas for extending the current network of protected areas in the Atlantic Forest. We achieved this objective by forcing the inclusion of current protected areas via a mask layer and looking at the top fraction of the study region, which included the protected areas plus the complementary areas. We generated three biodiversity management scenarios: (1) 'conservation only' in which we considered for prioritization only those cells with at least half of the area covered by forest; (2) 'conservation prior to restoration' in which forest remnant cells were forced into top priority fractions before cells with few or no remnants (this scenario represents a solution in which forest remnants would first be targeted for conservation, whereas sites that would require costly active restoration to maintain woody plant species populations would be targeted only second); and (3) 'unconstrained' scenario, in which no management is defined *a priori* and cells are ranked solely according to distribution, weight, and connectivity of features. All prioritization analyses were performed for the two climate change scenarios (RCP 2.6 and RCP 8.5), and two time periods (2050 and 2070), totaling 12 prioritization solutions. Prioritizations for 2050 and 2070 were highly correlated (0.98-0.99); hence, we present results for 2050 and those for 2070 are available only in Supporting Information (S5-S10).

Fraction of study region prioritized

To characterize and compare performance of prioritization solutions and management scenarios, we selected the top ranked cells at three different levels: 10%; 17%, and 20%. These levels represent different conservation targets of coverage for the Atlantic Forest, with 10% representing a more restrictive target, 17% corresponding to the Aichi Biodiversity Targets (CBD, 2010), and 20% representing an optimistic target.

Data processing and comparisons

We converted vector type spatial data (political-willingness, land cost, forest remnants and protected areas) to raster images at a spatial resolution of 5' for use in prioritization analyses. Political willingness and land cost raster cells were assigned their respective values from municipalities, which covered the center of the cell. Protected areas cells were assigned a value of 1 if completely or partially overlaid by protected areas and 0 otherwise, whereas forest remnant raster cells were assigned a value of 1 if at least half of the area was covered by forest and 0 otherwise.

Finally, we compared prioritization solutions in terms of the following measures: (i) number of species and average proportion of species' distributions remaining; (ii) comparisons of percentage lost or gained of feature representation obtained by the difference between solutions; and (iii) spatial correlation and overlap between the rankings of cells from different solutions. We used Dutilleul's (1993) method to estimate correct degrees of freedom and assess statistical significance of spatial correlations. Binomial generalized linear models (GLM) with a logit link function were used to determine whether representation of features among solutions differed statistically. Statistical analyses were performed with the R statistical environment (The R Foundation for Statistical Computing, 2014).

RESULTS

Species richness obtained by stacking ENMs predictions was not evenly distributed, reaching up to 1683 species per grid cell, with the highest values concentrated in the mid to southeastern portions of the Atlantic Forest (Fig. 1A). Of the 13,447 total grid cells, approximately 12% held high proportions of forest (Fig. 1B). Protected areas covered ~6% of the total number of cells, and only 4% of all grid cells were both protected and with high proportion of forest.

Prioritization solutions regardless of management scenarios and conservation target could not safeguard all woody plant species owing to potential climate-driven local extinctions. Priority sites in the 'conservation only' scenario represented less species than 'conservation prior to restoration' and 'unconstrained' schemes for both low and high greenhouse gas emission scenarios (Table 1). Priority sites for the 'conservation only' and 'conservation prior to restoration' scenarios were concentrated in the southern-southeastern portions of the Atlantic Forest where more forest remnants are present, whereas priority sites for the 'unconstrained' scenario shifted towards central and northeastern regions (Fig. 2 and 3). Prioritization solutions for the 10% conservation target protected a high number of species, and differed from conservation targets of 17% and 20% mostly in the proportion of species' distributions remaining and spatial configuration of top priority sites (Table 1, Fig. 3).

For a conservation area target of 10% under low and high greenhouse gas emission scenario 'conservation prior to restoration' covered smaller proportions of species' distributions, had increased probability of land-use conflicts, decreased political willingness to act, and increased costs of protecting land compared to 'unconstrained' scenarios (GLM: P =0.050 and P = 0.049, respectively). These

differences increased for targets of 17% ($P < 0.001$) and 20% ($P = 0.007$) under the low emission scenario, and for targets of 17% ($P < 0.001$) and 20% ($P = 0.009$) under the high emission scenario (Fig. 2, Table 2). Nonetheless, both management scenarios reduced constraint factors at a relative small expense to beneficial factors, when compared to a scenario in which only species' distributions were considered in prioritization (Tables S1 and S2).

Differences among prioritization solutions under low and high emissions were practically nil, with a slight tendency for low emission solutions to represent smaller mean percentages of species' distributions (differences: -0.34% to 0.04%), and having less political willingness to act (differences: -2.56% to 0.26%), but reducing land-use conflicts and economic costs (differences: -4.20% to 1.24% and -1.30% to -0.04%, respectively), depending on the conservation target (Table 3).

Top priority rankings for the 'conservation only' and 'conservation prior to restoration' management scenarios under low greenhouse gas emissions were similar to prioritizations under high greenhouse gas emissions, with correlations ranging from 0.95 to 0.99, whereas correlations for the 'unconstrained' scenario were lower, ranging from 0.60 to 0.91 (Table S3). Correlations between 'conservation prior to restoration' and 'unconstrained' rankings of top priority sites were variable, generally decreasing with increasing percentage of the Atlantic Forest protected. Correlations ranged from 0.28 to 0.90, depending on conservation target and greenhouse gas emission scenario (Table S4).

Spatial overlap between top 10% of priority rankings for prioritizations under low and high greenhouse gas emission scenarios was 96% in the 'conservation only' and 'conservation prior to restoration' management scenarios, whereas, for

'unconstrained' it was 89%. For conservation targets of 17% and 20%, 'conservation prior to restoration' had spatial overlaps of prioritization solutions of 95% and 93% under low and high emission scenarios, respectively, whereas 'unconstrained' obtained 88% and 86% overlaps. Spatial overlap between 'conservation prior to restoration' and 'unconstrained' for the top 10% priority rankings was 58% under low emission scenario and 56% under high emission scenario; for the top 17% of priority rankings, it was 47% under low emission and 46% under high emission scenario; finally, for the top 20% of priority rankings, it was 55% and 54% for low and high emission scenarios, respectively.

DISCUSSION

We emphasize the importance of preserving large existing forest remnants (Banks-Leite *et al*., 2014). However, we conclude that conservation of existing remnants alone, with regard to current and potential new protected areas, will not be sufficient to safeguard Atlantic Forest woody plant species under global environmental changes. Hence, the need for restoration to ensure the persistence of biodiversity across this biodiversity hotspot becomes clear.

Several conservation assessments and priority-setting initiatives have suggested conservation and restoration priorities within the Atlantic Forest. Previous initiatives vary greatly in terms of goals, taxonomic group, data and methods used for indentifying priorities (Pease *et al*., 2010). For instance, conservation and restoration priorities have been identified based on present potential distributions and population estimates of various taxonomic groups (Galetti *et al*., 2009; Murray-Smith *et al*., 2009; Trindade-Filho *et al*., 2012), centers of endemism (Silva *et al*., 2004), expert-based workshops (MMA, 2007), and detailed descriptions of remaining forests (Ribeiro *et al*., 2009;

Tambosi *et al*., 2014; Rappaport *et al*. 2015). Our approach complements previous assessments by making use of ecological and socio-economic variables, while taking into account climate and land-use changes, thus, allowing for a dynamic conservation strategy necessary to mitigate effects of global environmental changes.

Protected areas have been shown to be essential for maintenance of biodiversity and mitigation of climate change (Hannah *et al*., 2007; Araújo *et al*., 2011; Faleiro *et al*., 2013). Even though the current network of protected areas established in the Atlantic Forest is valuable in protecting woody plant diversity under different scenarios, our estimates show that it is insufficient to meet our targets, particularly in the northeast where large protected areas have not been established. The high number of species inside protected areas captured by the 'conservation prior to restoration' scenario, in comparison to the 'conservation only' scenario, stresses the importance of restoration efforts even inside protected areas (Ferretti & Britez, 2006).

Climate change and conversion of natural habitat to anthropogenic landscapes are considered the principal threats to biodiversity in the tropics (Asner *et al*., 2010; Brodie *et al*., 2012). Based on our dataset, a couple of examples strongly highlight the urgency of management actions. For instance, *Quiina paraensis* Pires, a tree species endemic to Brazil, and also occurring in the Amazon Basin, could be extirpated from the Atlantic Forest by 2050 owing to shifting climate conditions. *Pilocarpus microphyllus* Stapf ex Wardlew. an endangered medicinal plant used by both traditional communities and the pharmaceutical industry, could lose all natural populations to habitat reduction; as such its long term persistence depends on restoration of natural habitats.

The Atlantic Forest harbors a striking number of plant species, with estimates ranging between 13,979 and 20,000 species (Mittermeier *et al*., 2011; Forzza *et al*., 2012). Because of the high dimensionality and complexity of its biodiversity, we selected a subset (woody plant species) as surrogates to be used as an indicator group (Margules & Pressey, 2000). While small decreases in species numbers in our comparisons do not seem much (or statistically significant), they may in fact signal hundreds or even thousands more species, many of which still undocumented (Lewinsohn & Prado, 2005; Sobral & Stehmann, 2009; Forzza *et al*., 2012). Our findings reinforce the potential of climate change and habitat reduction to drive extinctions of tropical plant species. Indeed, even if all current Atlantic Forest remnants are protected, species could still be lost without appropriate efforts towards management and restoration.

Conservation targets are important to achieve goals in biodiversity conservation, yet they are rarely set and evaluated based on ecological knowledge (Soulé & Sanjayan, 1998; Tear *et al*., 2005). New protected areas are seldom established in a systematic manner, further endangering biodiversity (Venter *et al*., 2014). We found that, when a systematic planning scheme was applied to maximize conservation outcomes, targets of 17% and 20% captured most species and represented on average 26-34% of species' distributions. An alternative approach would be to set species-specific representation targets, based on area needs and population dynamics (Moilanen, 2007). But such information is scarce for most tropical plants greatly restricting its application. Given that forest remnants covered only 12% of the original Atlantic Forest extent considered here, conservation targets of 17% and 20% can only be achieved via restoration of degraded habitats.

The ‘conservation only’ scenario represent sites with high amount of forest in which establishing nature reserves, excluding anthropogenic impacts and promoting forest regeneration would likely enable the persistence of woody plant species (Holl & Aide, 2011; Zwiener *et al*., 2014). These sites could also be focus of payment for ecosystem services in which land owners receive a financial support to set aside private land (Banks-Leite *et al.*, 2014). We did not take into consideration local and landscape factors (e.g. the spatial distribution of remnants, unforested matrix, successional stage of forests and presence exotic invasive species) which could further constrain the occurrence and persistence of species in these sites. Our estimate for the potential of forest remnant cells to sustain biodiversity is thus quite optimistic. Forest remnant cells could be seen as primary targets for conservation but additional intervention may also be necessary.

Although it would be desirable to have all sites with natural habitat included before selection of priority sites to expand a reserve network, such an ideal situation is, however, often unfeasible in much of the tropics. By comparing the ‘unconstrained’ scenario, in which the algorithm is allowed to rank sites solely based on presence of protected areas, distribution, weights, and connectivity of features, with the ‘conservation prior to restoration’ scenario, in which top priority sites are forced into cells containing protected areas and forest remnants, we could assess impacts of habitat reduction on prioritization solutions. The representation of beneficial factors (biodiversity and political willingness) and minimization of constraint factors (land use and cost) were clearly affected by availability of forest remnants. In an ideal situation, the most effective prioritization solution would include top priority sites in regions where large forest remnants are no longer available for conservation. We found that the spatial pattern of habitat degradation has important implications for conservation

planning, negatively affecting representation of biodiversity and implying higher costs and reduced efficiency.

Many factors have to be taken into account when trying to predict how future climate change will affect biodiversity (Thuiller *et al*., 2008). The intensity of climatic change is a key variable (Diniz-Filho *et al*., 2009). Contrary to our expectations the two climate change scenarios did not differ substantially in terms of the spatial configuration of top priority sites and representation of features. We reinforce, however, that by using only species with ≥ 15 records, we excluded poorly sampled and highly endemic species (693), which may be the species most vulnerable to environmental changes (Moritz & Agudo, 2013). Exclusion of rare species may systematically underestimate certain important sites (Platts *et al*., 2014), possibly obscuring differences between climate change scenarios.

In this study we explored the first stages of a multi-stage process, which aims at effective and systematic conservation of biodiversity. We show that if a systematic planning scheme considering complementary management actions is applied to the Atlantic Forest, reaching the 17% Aichi biodiversity target may constitute an important step towards protecting woody plant species. Most tropical forests face similar threats related to habitat reduction, fragmentation, and climate change, so we believe that our results may represent patterns applicable in other threatened tropical forests. Expansion of protected areas will be necessary to compensate for altered species' distributions induced by climate change; however, additional efforts involving habitat restoration are urgently required to maintain Atlantic Forest biodiversity into the future.

ACKNOWLEDGMENTS

We are thankful to the many herbaria that form the speciesLink network for sharing their invaluable data. We would also like to thank Narayani Barve and Andrés Lira-Noriega for assistance with R scripts, GIS operations, and niche modeling. RL's research has been funded by CNPq (grants #308532/2014-7, 479959/2013-7, 407094/2013-0), Conservation International Brazil, and the O Boticário Group Foundation for the Protection of Nature (PROG_0008_2013). MCMM received grant from CNPq (# 304650-2012-9) and VPZ received scholarship from the Brazilian Education Council (CAPES).

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Table 1. Number of species and average proportion of species ranges remaining, in parenthesis, within top priority sites for different management scenarios. Comparisons are shown for priority sites within current protected areas (PAs) and for different conservation targets (10%, 17% and 20%) in the Atlantic Forest under low and high greenhouse gas emission scenarios in 2050.

Management scenario	Low emission				High emission			
	PAs	10%	17%	20%	PAs	10%	17%	20%
Conservation only*	2219 (0.37)	2253 (0.85)	-	-	2221 (0.37)	2253 (0.85)	-	-
Conservation prior to restoration	2251(0.09)	2253 (0.15)	2254(0.26)	2254 (0.32)	2251 (0.09)	2253 (0.15)	2254(0.26)	2254 (0.32)
Unconstrained	2251 (0.09)	2254 (0.17)	2254(0.30)	2254 (0.34)	2251 (0.09)	2254 (0.17)	2254(0.30)	2254 (0.34)

*comparisons restricted to current forest remnants; comparisons of 17% and 20% top priority sites are not possible for the 'conservation only' management scenario, given that only 12% of the Atlantic Forest original extent is available for conservation

Table 2. Comparisons of representation of each feature between the management scenario of conservation of forest remnants prior to restoration of degraded habitat ('conservation prior to restoration') and no *a priori* definition of action ('unconstrained') within top priority sites for different conservation targets in the Atlantic Forest. Values represent the difference (loss is negative, gain is positive) in feature representation achieved by the conservation prior to restoration scenario under low and high greenhouse gas emission scenarios in 2050.

Features	Low emission			High emission		
	10%	17%	20%	10%	17%	20%
Biodiversity	-1.60	-3.86	-2.62	-1.66	-3.90	-2.57
Land use	0.85	6.79	6.51	1.04	4.28	3.89
Political willingness	-1.54	-2.57	-2.96	-1.02	-3.93	-5.39
Land cost	1.92	36.67	36.33	1.97	36.53	35.94

Table 3. Comparisons of representation of each feature between low and high greenhouse gas emission scenarios within top priority sites for different management scenarios and conservation targets in the Atlantic Forest. Values represent the difference (loss is negative, gain is positive) in feature representation achieved by the low greenhouse gas emission scenario in 2050.

Features	Conservation only*			Conservation prior to restoration			Unconstrained		
	10%	17%	20%	10%	17%	20%	10%	17%	20%
Biodiversity	-0.34	-	-	-0.02	-0.02	-0.01	-0.08	-0.06	0.04
Land-use	-4.20	-	-	-0.50	1.24	0.88	-0.31	-1.27	-1.74
Political-willingness	-0.99	-	-	-0.80	0.26	-0.13	-0.28	-1.10	-2.56
Land cost	-1.30	-	-	-0.18	-0.04	-0.07	-0.13	-0.18	-0.46

*comparisons restricted to current forest remnants; comparisons of 17% and 20% top priority sites are not possible for the ‘conservation only’ management scenario, given that only 12% of the Atlantic Forest original extent is available for conservation

Figure Legends

Figure 1. Woody plant species richness viewed in terms of summed results of ecological niche models, and geographic distribution of forest remnants in the Atlantic Forest. In the latter map, orange cells represent sites with high proportion of forest remnant considered in the biodiversity management scenarios.

Figure 2. Nested hierarchical ranking of conservation priorities, current protected areas (PAs) and performance graphs for different management and greenhouse gas emission scenarios forecasted to 2050. Performance graphs indicate representation of each feature at a given proportion of the landscape protected. Graph legend: Woody plant species (solid line); forecasted land-use (dotted line); political willingness to act (short-dashed line); land cost (long-dashed line).

Figure 3. Spatial distribution of priorities for conservation targets of 10% (red), 17% (yellow) and 20% (blue) along with current protected areas (PAs) for different management and greenhouse gas emission scenarios forecasted to 2050.

Fig. 1

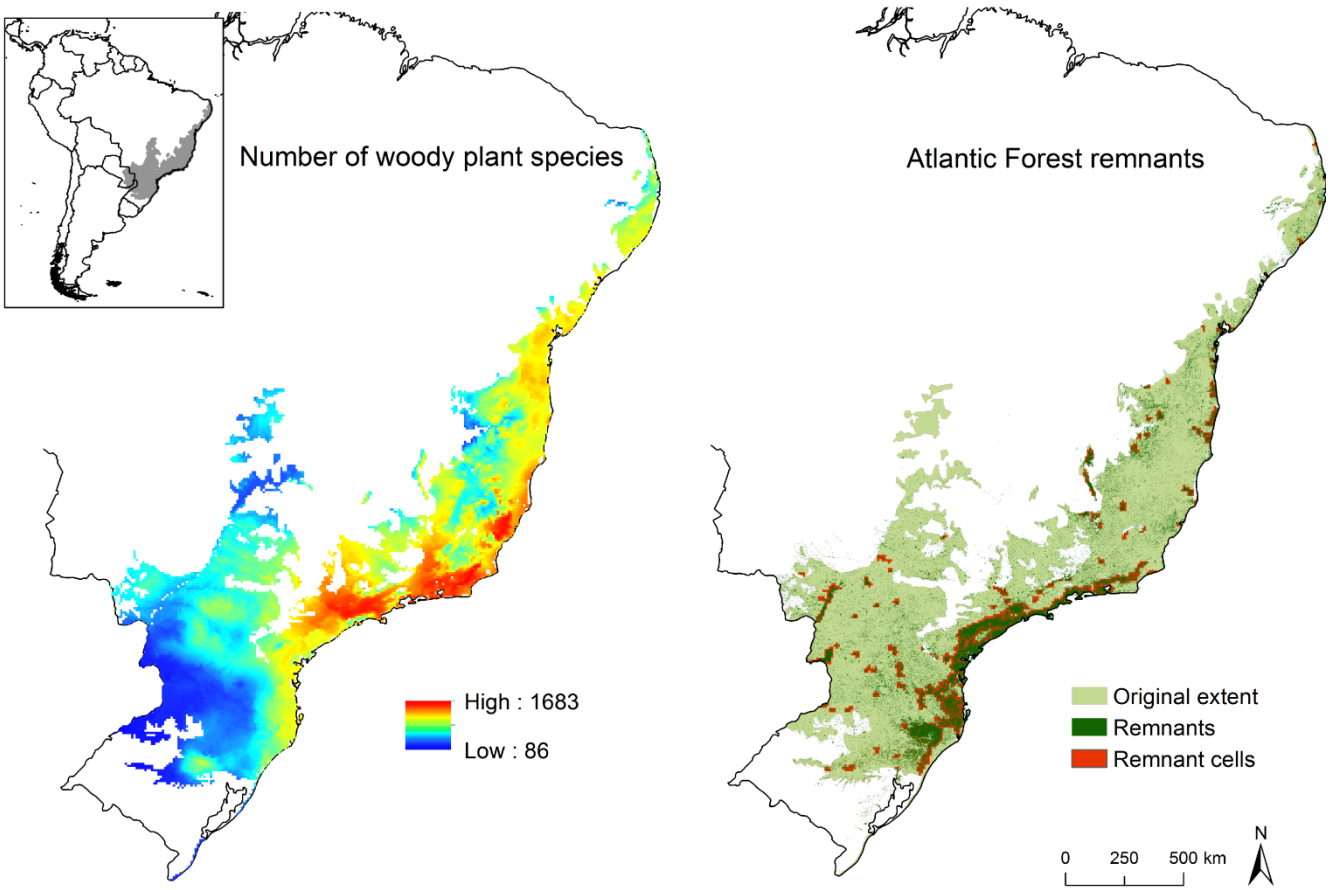

Number of woody plant species
High : 1683
Low : 86
Atlantic Forest remnants
Original extent
Remnants
Remnant cells
0
250
500 km
N

Fig. 2

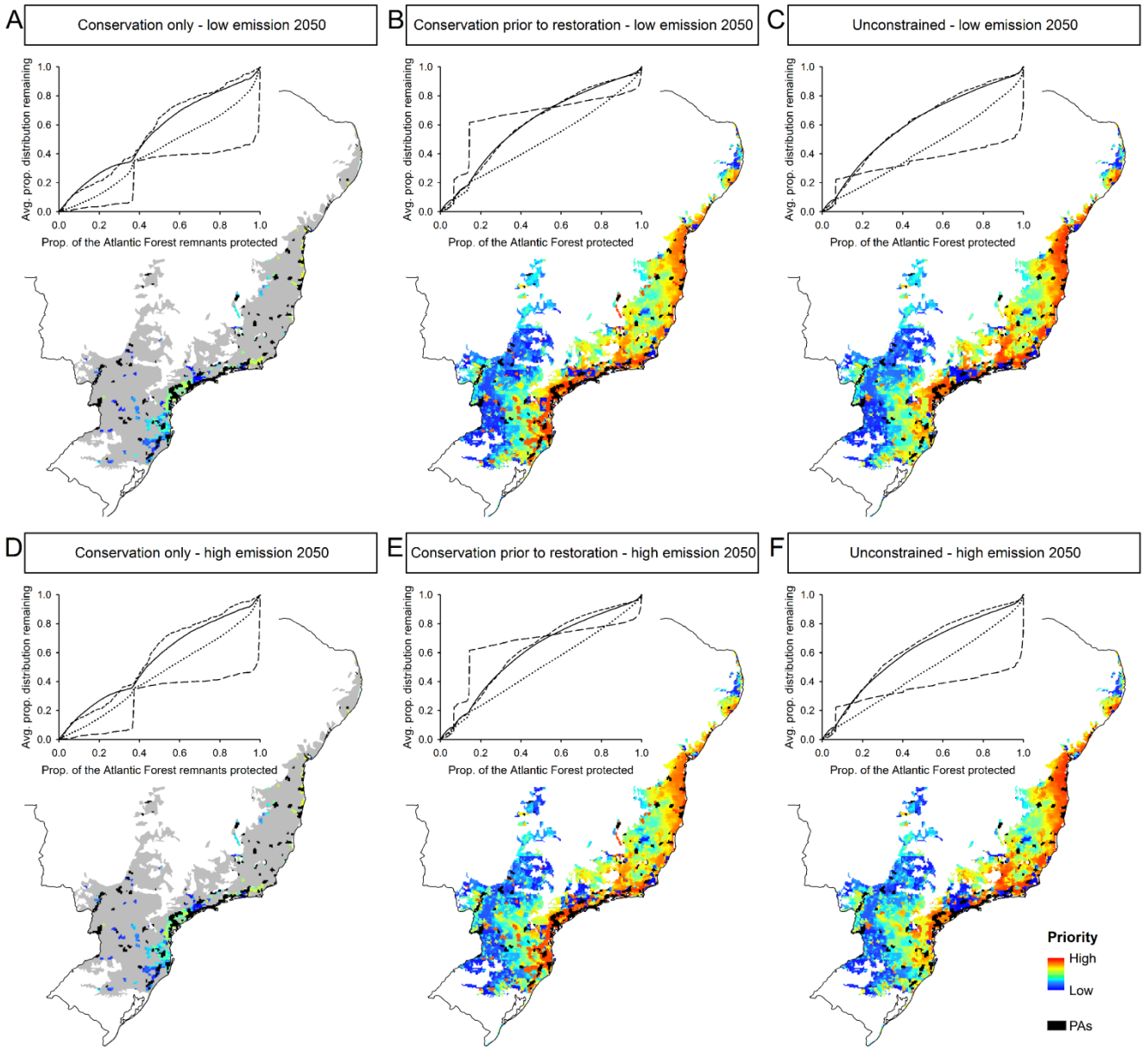
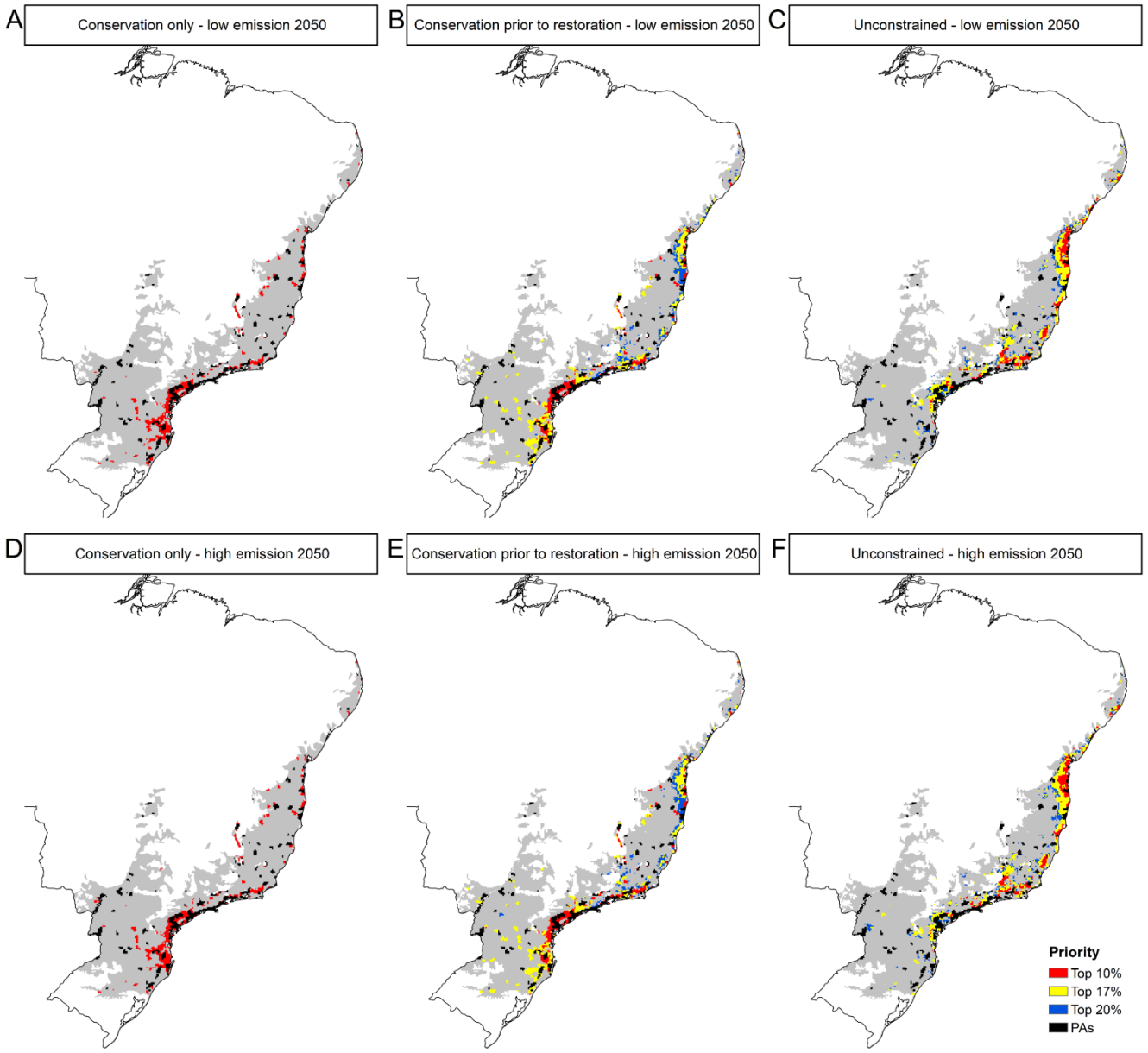

A
Conservation only - low emission 2050
B
Conservation prior to restoration - low emission 2050
C
Unconstrained - low emission 2050
D
Conservation only - high emission 2050
E
Conservation prior to restoration - high emission 2050
F
Unconstrained - high emission 2050
Avg. prop. distribution remaining
Prop. of the Atlantic Forest remnants protected
Prop. of the Atlantic Forest protected
0.0
0.2
0.4
0.6
0.8
1.0
Priority
High
Low
PAs

Fig. 3


A
Conservation only - low emission 2050
B
Conservation prior to restoration - low emission 2050
C
Unconstrained - low emission 2050
D
Conservation only - high emission 2050
E
Conservation prior to restoration - high emission 2050
F
Unconstrained - high emission 2050
Priority
Top 10%
Top 17%
Top 20%
PAs

4 CAPÍTULO 3

Mudanças climáticas como fator determinante de homogeneização biótica: Mecanismos e conseqüências para a conservação de plantas lenhosas na Mata Atlântica

*Capítulo formatado de acordo com as normas da revista científica *Global Change Biology*

Climate change as driver of biotic homogenization: Mechanisms and consequences for conservation of woody plants in the Atlantic Forest Biodiversity Hotspot

Running head: Climate change and biotic homogenization

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Keywords: Range-diversity plots, tropical forests, biodiversity, greenhouse gas emissions, community structure, ecological niche modeling

Type of paper: Primary Research Article

Abstract

Climate change presents a major threat to biodiversity yet its potential effects on the organization of highly diverse species assemblages are poorly understood, impeding the formulation of effective conservation strategies. Here we applied ecological niche modeling in association with a recently introduced macroecological analytical tool and robust null models to assess spatial-temporal changes of biodiversity. We estimated the potential distribution of 2,255 woody plant species and explored changes in diversity, range size and covariance in species composition of assemblages under contrasting climatic scenarios and at different scales. We also explored diversity changes within protected areas and inferred their potential to conserve biodiversity in the future. Our results show that despite general increase in local richness, beta diversity decreases at larger scales, the increased similarity among sites was accentuated in more sever climate change scenarios. Reduction of beta diversity was accompanied by increment of the mean range size of species within a site, suggesting that the likely broad scale mechanism underlying the observed patterns is the expansion of current species' distributional limits rather than extinction or retraction of local endemics. However, these changes were not constant or homogeneous across space. Likewise, assemblages within protected areas presented higher similarity, increased mean range size and invariability of richness through time indicating potential compositional turnover promoted by the expansion of widespread species at the expanse of local endemics. Our findings suggest that the current diversity structure of woody plant assemblage in the Atlantic Forest is prone to structural reorganization due to climate change which has high potential to increase biotic homogenization in the future.

Keywords: Range-diversity plots, tropical forests, biodiversity, greenhouse gas emissions, community structure, ecological niche modeling

Introduction

Climate change is increasingly recognized as a major threat to current biodiversity and human well-being and its effects have already been observed across multiple biological systems (Thomas *et al*., 2004; Thuiller, 2007; Cahill *et al*., 2012). Evidence suggests that species respond individualistically to shifting environmental conditions which may reorganize diversity patterns and jeopardize provision of ecosystems services in a warmer future (Keith *et al*., 2009; Cardinale *et al*., 2012; Urban *et al*., 2012; Thomas, 2013; Thornton *et al*., 2014). Assessment of climate change impacts on spatial diversity patterns is thus critical to formulation of effective conservation strategies and better understanding of the climatic role in global environmental change processes (Hansen *et al*., 2001; Thomas *et al*., 2004; MEA, 2005).

Global temperatures are increasing and reaching levels unprecedented over decades to millennia. Forecasts project even greater changes for the end of the 21st century (IPCC, 2013). Climate change is already affecting organisms across a wide range of taxonomic and functional groups by shifting distributions, altering their phenology and even leading to extinction (Pounds *et al*., 1999; Thomas *et al*., 2004; Parmesan, 2006; Lenoir *et al*., 2008; Moritz *et al*., 2008; Hiddink *et al*., 2015). Although intense social, political and scientific debate has been placed on possible mechanism and threats imposed by climate change (Thuiller, 2007; Pettorelli, 2012; Garcia *et al*., 2014; Thornton *et al*., 2014), the reorganization of biodiversity and impacts for society are not yet fully understood, particularly in the tropics (Thuiller *et al*., 2008; Willis & Bhagwat, 2009; Wright *et al*., 2009; Corlett, 2011; Thornton *et al*., 2014). Assessing the consequences of climate change in the most vulnerable and species rich regions of the world (e.g. megadiverse countries, Mittermeyer, 1988) is therefore of extreme importance to support management decisions and improve conservation of biodiversity and derived ecosystem services (Barnosky *et al*., 2012; Cardinale *et al*., 2012).

It is long recognized that species respond to abiotic conditions and have distinctive environmental requirements (Grinnell, 1917; Hutchinson, 1957). Among variables comprising species environmental niche, climate is widely knowledge as important component acting at broad spatial scales with strong influence on distributional patterns (Cain, 1971; Woodward, 1984). Indeed, paleoecological and current evidence suggests that shifting climatic conditions have the potential to modify species distribution and by extension community structure (Williams & Jackson, 2007). Many studies have explored shifts in individual species' climatic suitability and geographic range, but only few studies have examined the consequences of individual shifts to changes in community composition across space and time (Berg *et al*., 2010; Sheldon *et al*., 2011; Dornelas *et al*., 2014).

Shifting climatic conditions have differentiated effects on species. While some species may benefit from reduction of climate related barriers and expand their ranges, others may suffer from imposition of intolerable novel climates and contract ranges to climatic suitable areas (Moritz & Agudo, 2013). The process by which widespread species gradually replace local endemics leading to decrease beta-diversity across space and over time has been termed biotic homogenization (McKinney & Lockwood, 1999; Olden & Poff, 2003; Olden & Rooney, 2006). Climate change can potentially enhance biotic homogenization by promoting range expansions of species with broad environmental niches and forcing range contractions of species with narrow niches, thus mixing the composition of once disparate biotas (Olden *et al*., 2004).

Biotic homogenization is usually quantified by pair-wise comparisons of genetic, taxonomic or functional similarity of two or more locations over a specified time interval (Olden & Rooney, 2006). Spatial-temporal patterns of diversity and similarity may be summarized using a variety of indices (Tuomisto, 2010; Anderson *et al*., 2011), by combining different metrics of biodiversity into a single framework the analysis may reveal patterns from

different perspectives and infer on processes generating them. Mathematical relationships linking species richness and range size were recently introduced to describe geographical patterns of biodiversity based on species' presence and absence data (Arita *et al*., 2008; Arita *et al*., 2012). Range-diversity plots (hereafter 'RD plot') are analytical frameworks that make use of these relationships displaying simultaneously information about the species number, ranges and covariance among localities (Arita *et al*., 2008). Linking the abstract scatter-plots with maps provides a better visualization of patterns, thus allowing for a more thorough analysis of the multifaceted aspect of diversity (Soberón & Ceballos, 2011).

Here we explore current and future patterns of woody plant diversity in the Atlantic Forest biome, one of the most biologically rich forests in the world and a global 'hotspot' for biodiversity conservation (Myers *et al*., 2000; Mittermeier *et al*., 2011). We apply ecological niche modeling (ENM) to assess species' climatic suitability in the present and future scenarios, and assuming a relationship between environmental niche and geographic distributions we infer on possible effects of shifting climatic conditions as driver of diversity changes and biotic homogenization (taxonomic) using RD plots. More specifically, we explore the current and future spatial patterns of species richness, range size and covariance in composition across different Atlantic Forest ecoregions and under contrasting climate change scenarios. We hypothesize that the invasion/expansion of widespread warm climate adapted species at the expanse of endemic narrowly distributed species results in reduction of beta diversity, which is observed by an increase in species mean covariance and range distribution over time. Furthermore, we explore potential diversity changes within current protected areas in the Atlantic Forest and infer their potential to conserve biodiversity over time.

Materials and methods

Study region

The Atlantic Forest comprises a unique series of ecosystems originally extending over 1.5 million km^2 on the Brazilian coast and in continental inland areas (Stehmann *et al*., 2009; Forzza *et al*., 2012). Its complexity and floristic differentiation are related to the wide geographic and environmental gradients (Oliveira-Filho & Fontes, 2000), combined with anthropogenic disturbances and historical factors (Tabarelli *et al*., 2005; Carnaval & Moritz, 2008; Fiaschi & Pirani, 2009). For instance, latitude ranges from 5^oN to 33^oS, longitude from 35^oW to 52^oW, elevation goes from sea level to about 2,200 meters (IBGE, 1992), annual precipitation and mean temperature varies from 800 mm to 4,000 mm and 5 ^oC to 25 ^oC, respectively (Stehmann *et al*., 2009). The Atlantic Forest shows floristic similarities with the Amazon Forest and Caatinga in the North (Oliveira-Filho *et al*., 2005; Mori *et al*., 1981; Oliveira-Filho & Ratter, 1995) and it is influenced by the flora of the Andes and elements of the ancient southern Gondwana in the South (SanMartín & Ronquist, 2004). Currently only 11 to 16% of this rich forest biome remains, mostly in small fragments of remnant and secondary forest (Ribeiro *et al*., 2009).

Woody plant species and occurrence data

We chose the focal species based on compiled checklists of 300 field inventories distributed across the Atlantic Forest (Zwiener et al., submitted). The checklists comprised 2,948 species from 110 families; all species passed through an extensive review process aiming at reducing nomenclature and identification inconsistencies. We obtained species occurrence records from the field inventories which were complemented with geo-referenced herbarium voucher specimens retrieved from *species link* (http://splink.cria.org.br/), an electronic database of Brazilian primary biodiversity data currently containing over five million geo-referenced records from 377 herbariums and natural museums.

We removed duplicated records and errors associated to georeferencing by comparing the geographic location of each record with range limits established by specialists (ranges provided in floradobrasil.jbrj.gov.br). To reduce effects of sampling bias and spatial autocorrelation on model performance (Hijmans, 2012; Boria *et al*., 2014) we excluded all but one record from the same species within the vicinity of ~20km. Initially, we obtained a total of 673,096 geo-referenced records for 2,948 species, after the subsetting and spatial filtering procedures we retained 286,798 records. In addition, we only considered for the modeling analyses species with a minimum of 15 records which further reduced the number of plant species to 2,255 contained in 285,642 records.

Environmental variables

Environmental variables for current and future climate projections were obtained from WorldClim database (http://www.worldclim.org; Hijmans *et al*., 2005) at a spatial resolution of 5'. Variables for future climate projections were based on the IPCC Fifth Assessment Report from which we selected three global climate models (CCSM4, GISS-E2-R and MIROC5) and two contrasting representative concentrations pathways (RCP2.6 and RCP8.5) for the year 2050 (average for 2041-2060) and 2070 (average for 2061-2080). To reduce dimensionality and collinearity of environmental layers we performed principal component analysis (PCA) based on a correlation matrix of standardized variables. PCA was performed with all current 19 'bioclimatic' variables and the values were predicted to future climate projections. We used the first six principal components, which accounted for >95% of the variation, to characterize the present and future environmental conditions across the study region.

Ecological Niche Modeling - ENM

We used ENM to identify sites environmentally suitable for the persistence of individual species in the present and in future climate scenarios. ENM has been widely used to infer species potential distributional areas and represents an important tool for assessments of climate change impacts (Elith & Leathwick, 2009; Peterson *et al*. 2011; Araújo & Peterson, 2012).

Because dispersal limitation plays a crucial role in the distribution of organisms and should be considered in ENM, we used a calibration area that reflects the geographical region that has been historically accessible to the species (Barve *et al*., 2011). Here we have assigned the calibration area for each species by plotting occurrence points in geographical space, comparing the distribution of points to ecoregions (Olson *et al*., 2001), historical climatic stable areas (Fig. 2 from Carnaval & Moritz, 2008) and range limits established by specialists (floradobrasil.jbrj.gov.br). Calibration areas ranged from the tropical and sub-tropical region east of the Andes for widely distributed species (e.g., *Tapirira guianensis* Aubl.) to relatively small areas for narrowly distributed endemic species (e.g., *Pseudoxandra bahiensis* Maas).

We used the maximum entropy, 'Maxent', method (Phillips *et al*., 2006) implemented in the R-package dismo (Hijmans *et al*., 2012) to construct niche models. We chose Maxent over other available methods for ENM given its high performance and adequacy to presence-only data (Elith & Graham, 2009; Elith *et al*., 2010; Peterson *et al*., 2011). Used settings were five bootstraps replications, raw output and a threshold of 5% lower values of training presences over the median estimate to produce binary predictions (Peterson *et al*., 2011; Merow *et al*., 2013). Other settings were kept as default.

We obtained the final estimates of climatically suitable areas for each species in 2050 and 2070 by overlaying thresholded projections from the three global climate models within the same RCP and considering sites in which all three estimates coincided. The estimates are

referred to as 2650 and 2670 for projections base on scenarios considering low greenhouse gas emissions (RCP2.6) in 2050 and 2070, respectively, and 8550 and 8570 for projections based on high greenhouse gas emissions scenarios (RCP8.5) in 2050 and 2070, respectively.

Presence-absence matrices and summary metrics

We constructed a site × species presence-absence matrix (PAM) for each climate scenario and time period by overlying the estimated distribution of each species at the native spatial resolution of the bioclimatic data (5'). This process resulted in five PAMs of 14905 sites × 2255 species one for each climatic conditions. For each PAM we compared Whittaker's beta diversity, mean species richness and range sizes. We obtained Whittaker's beta diversity by simply dividing the total number of species (S) by the average local species richness. Similarly, Whittaker's beta diversity was obtained by dividing the total number o sites (N) by the average range size of all species. Based on this relationship we compared the average percentage of sites occupied by species which is equivalent to the average percentage of species occurring on each site.

Range-Diversity plots

Range-diversity plots depict information on species richness, range size and covariance simultaneously based on four numeric vectors: (i) the proportional (to S) number of species in every one of $j = 1, 2, \ldots, N$ sites, that we denote by $\boldsymbol{s}$ and (ii) the proportional (to N) range size of every one of $i = 1, 2, \ldots, S$ species, denoted by $\boldsymbol{n}$. The mean of any of these two vectors gives the inverse value of Whittaker's beta diversity (Arita *et al*., 2008); (iii) The mean proportion of species inhabiting every site in the range of species *i* is called the ''diversity field'' (Arita *et al*., 2008), denoted by $\boldsymbol{D}$, which measures how rich in species are the localities composing the range of a given species; (iv) The mean proportional (to N) range of the species inhabiting a site has been termed the ''dispersion field'' (Graves & Rahbek,

2005), denoted by ***R***, which measures how widespread are the species living on a given site. Plotting ***n*** × ***D*** and ***s*** × ***R*** constitute the per-species and per-site RD plot, respectively. We obtained a per-site RD plot for each PAM to estimate in each case the beta diversity and limit associated to the maximum covariance as measures of species potential for co-occurrence in each climatic scenario (see Arita *et al*., 2008; Soberón & Ceballos, 2011 for details). Axes in the per-site RD plot correspond to the proportional species richness of sites in the ordinates, and to the mean proportional per-site range size in the abscissa. The distribution of points in the RD plot is determined by biological and mathematical constrains related to the minimum and maximum species richness and range size, while the central tendency is determined by Whittaker's beta diversity of the entire community, which is equivalent to the proportional fill (total occurrences/N) of the PAM (Arita *et al*., 2008). The overall dispersion of points in the plot depends on the covariance among sites, which is determined by the number of sites with which each individual site shares its species. The points to the right and left of the vertical line (1 / beta diversity) have positive and negative covariance, respectively.

Mean proportional range size and proportional species richness obtained from the RD plot analyses were used to explore the overall species beta diversity and covariance. To visualize regions in the Atlantic Forest having species assemblages with high richness-and-small ranges and low richness-and-large ranges we followed a similar approach as in Villalobos *et al*. (2013) by selecting the sites that correspond to the extreme quartiles of the two axes in the RD plot, and linking those sites to geographical regions, thus providing a detailed evaluation of the characteristics of species assemblages. We further explored current patterns of species diversity and range sizes in the Atlantic Forest by identifying sets of points in the RD plot that correspond to the different Atlantic Forest ecoregions (*sensu* Olson *et al*., 2001).

The potential effects of contrasting climate change scenarios on the Atlantic Forest entire species assemblage were assessed by comparing the dispersion of points in the RD plot between current climatic conditions and all future scenarios. Specifically, we contrasted the lines of 1 / beta diversity and maximum covariance among all scenarios, which simplify the visualization of point dispersion in the plot (Arita *et al*., 2008).

To assess effects of climate change on species assemblages of different regions, we contrasted averages and standard deviations of species richness, range sizes and covariance in composition of sites within each ecoregion obtained from current and future climate projections. Finally, we used notched box plots (Chambers *et al*., 1983) to compare changes of the same metrics within strict protected areas in the Atlantic Forest (data available at http://mapas.mma.gov.br/i3geo/datadownload.htm). All RD plot analyses were conducted with the R statistical environment (The R Foundation for Statistical Computing, 2014) and spatial visualizations were done in ArcMap.

Null models

In order to determine statistical significance of values obtained from our RD plot analyses, we generated 100 randomized PAMs for each climatic scenario and compared the probability with which random values were similar to observed ones, assuming a significant difference at $p \leq 0.01$. The randomization algorithm creates permutations of the PAM that hold marginals constant for both species totals and site totals to produce results that are more closely related to the observed PAM, as opposed to only fixing one or none of the marginals (Gotelli, 2000). It uses a fill-based approach to produce the random matrices and overcomes the scaling limitations observed in other algorithms (Cavner *et al*., 2012) by operating on each cell of the new matrix in parallel (Grady *et al*., in preparation).

For each cell, a random number is generated and presence is determined by comparing the number to a threshold computed using the proportional fill of presences in the row and the column which the matrix cell is located. Because each cell can be evaluated as an atomic operation, the initial fill of the matrix can be done in parallel. A second step corrects rows and columns that were either over, or under, predicted. The end result is an algorithm that generates any permutation of a random matrix, with the specified marginal, with equal probability. The algorithm is part of the Lifemapper Project (http://lifemapper.org) and its current implementation is written in Python programming language.

Results

Current plant diversity patterns

The Atlantic Forest woody plant assemblage had a Whittaker's beta of 2.99 and sites contained, on average, 33% of the species. Similarly, woody plant species occurred, on average, in 33% of sites (Table 1). Under current climatic conditions the region with highest species richness corresponded to sites near the coast of the Atlantic Forest, whereas, the lowest species richness was found towards the interior of the continent and in the southernmost part of the biome. Sites with the smallest mean proportional range size precisely corresponded to the region with highest species richness and sites with the largest mean ranges were located in species poor regions (Fig. 1). All sites showed positive covariance, indicating that they have species in common.

The ecoregions comprising the Atlantic Forest showed concise groups of points in the RD plot with the exception of Atlantic Coast restingas in which the corresponding points were spread apart in different sectors of plot (Fig. 2). The ecoregions with high number of species and small mean range size were Serra do Mar and Bahia coastal forests, with the latter having the smallest range sizes. In the opposite end of the RD plot were Alta Paraná Atlantic forests

and Araucaria moist forests with low species richness and large mean range size. The ecoregions with higher covariances were Alta Paraná Atlantic forests, Araucaria moist forests and Bahia interior forests, whereas, Bahia coastal forests, Pernambuco coastal and interior forests and Atlantic Coast restingas showed the smallest covariances (Fig. 2).

Plant diversity patterns under climate change and within protected areas

The overall Whittaker's beta diversity, average richness, range size and covariance of sites differed between current climatic conditions and future scenarios, with a clear tendency of increased covariance, richness and ranges, and reduced beta diversity in the future (Table 1; Fig. 3). In all cases we observed a dispersion of points with positive covariance.

Species richness within ecoregions obtained from projections to future climate scenarios was highly variable with a tendency to increase in comparison to current values, exceptions were Bahia interior and coastal forests in which richness decreased or remained constant depending on future climate scenario (Fig. 4). Estimates of mean range size and covariance within ecoregions presented a consistent tendency towards larger values (Fig. 4). Significant increase in mean range size was observed between current and 8570 conditions for Pernambuco interior forests, Pernambuco coastal forests, Bahia coastal forests, and Bahia interior forests; and for covariance between current and 8570 conditions for Pernambuco coastal forests, Pernambuco interior forests and Araucaria moist forests.

In comparison to current climate conditions sites within strict protected areas under climate change scenarios showed increased mean range size and covariance. Conversely, species richness did not differ between current and future conditions (Fig. 5).

Null models

Observed results showed a departure from values obtained under the null models. While beta diversity of the entire assemblage did not change because the randomization algorithm leaves PAM dimensions and fill constant, covariance values were higher than random in all cases ($p \leq 0.01$), implying changes in the parameters of variation around the mean. For instance, the shape of the species-richness frequency distribution and the horizontal location of points in the RD plot.

Discussion

Here we assessed spatial and temporal changes of diversity patterns in a megadiverse tropical forest hotspot. Comparing species assemblages obtained from ecological niche models allowed us to dissect the relative role of climate as driver of biodiversity changes at multiple scales and across different time periods. Our findings suggest that the current diversity structure of woody plant assemblage in the Atlantic Forest is prone to experience reorganization due to shifting climatic conditions, increasing biotic homogenization.

The Atlantic Forest presented a RD plot structure characterized by points (sites) with positive covariance, following a negative slope with the mid region near the maximum covariance line (Fig.1). These characteristics have been depicted as evidence of nested systems (Arita *et al*., 2008; Arita *et al*., 2012), in which assemblages of less species-rich sites contain subsets of progressively richer sites (Patterson, 1987). Moreover, because RD plots present information based simultaneously on distribution of species and diversity of sites, our results show that specious sites contain species with both narrow and wide distributions, whereas, species poor sites contain a subset of widely distributed species. Although conservation actions aiming at species-rich sites may effectively capture both widely distributed and endemic species, low richness-and-large ranges species assemblages may play a crucial role by providing ecosystem services, habitat to other life forms and promoting

landscape connectivity, therefore, they must also be carefully evaluated for successful conservation of the Atlantic Forest (Rockström *et al*., 2009; Perrings *et al*., 2010).

The eight ecoregions considered here as comprising the Atlantic Forest have uneven distribution and sizes. Overall, these ecoregions encompass different environmental conditions and species assemblages (Oliveira-Filho & Fontes, 2000; Marques *et al*., 2011), which in the RD plot could be distinguished as relatively concise groups with different values of species richness and range sizes, giving support to the awareness of the Atlantic Forest as a complex of ecosystems (Rizzini, 1979; Scarano, 2009). Furthermore, regions with high covariances have been hypothesized and associated, in a ecological context, to the existence of suites of species adapted to extensive and spatially autocorrelated environments, whereas regions with small covariances would correspond to assemblages composed of species in the border of the available land, or inhabiting very unique environments (Soberón & Ceballos, 2011). In fact, the Atlantic Forest ecoregions showing higher covariance (e.g., Alta Paraná Atlantic forests, Araucaria moist forests and Bahia interior forests) are the largest in size and correspond to inland areas marked by climate seasonality (Kamino *et al*., 2008; Santos *et al*., 2011), conversely, ecoregions with lower covariance (e.g., Pernambuco inerior and coastal forests, Bahia coastal forests and Atlantic Coast restingas) are smaller and spatially constrained by the ocean, mountains and desert-like landscape (i.e. Caatinga).

We observed temporal changes of diversity patterns captured by different and complementary metrics. The overall beta diversity of the Atlantic Forest woody plant assemblage presented systematic loss when current estimates were contrasted with future climatic scenarios, further, the increased similarity among sites was accentuated in more sever climate change scenarios. The observed reduction in beta diversity was accompanied by an increase in maximum covariance indicating that the likely broad scale mechanism underlying the predicted biodiversity changes in the Atlantic Forest is the expansion of current species

distributional limits rather than extinction or retraction of local endemics. These results are supporting the theoretical predictions of increase species richness at local scales and decrease diversity at larger scales (Dornelas *et al*., 2014; McGill *et al*., 2015; Teyssèdre & Robert, 2015).

Notwithstanding, we found that temporal diversity changes varied across space. Ecoregions experienced different intensity and even direction of changes. While most ecoregions presented a slight tendency to increase richness, Bahia interior and coastal forests had constant richness or a tendency of species loss in future climatic conditions. Conversely, mean proportional range size and covariance presented a consistent tendency of higher values in the future. Combined these results show that some regions may experience decrease of beta diversity associated to invasion of widely distributed generalist species whereas others may suffer from the synergy of range expansion of adapted species and local extinction of narrowly distributed intolerant species.

Tropical forests are already suffering drastic biodiversity declines with important consequences for ecosystem functioning (Hooper *et al*., 2005; Butchart *et al*., 2010; Galetti *et al*., 2013). Habitat fragmentation and degradation are considered the principal causes of current declines (Silva & Tabarelli, 2000; Brooks *et al*., 2002; Ribeiro *et al*., 2009). In such highly impacted landscapes protected areas play a crucial role for the conservation of remnants and provision of ecosystem services (Isbell *et al*., 2011). Our results stress for the potential of climate change to enhance biotic homogenization within current protected areas, where widespread species invasions could buffer local species extinctions and thus maintain consistent levels of richness at the expense of beta diversity. Additional anthropogenic threats (i.e. exotic species introduction) in association to climate change could further compromise the protection of biodiversity in the future.

Inference about the consequences of climate change on highly diverse tropical assemblages at larger spatial scales has remained mostly on theoretical grounds (Malhi *et al*., 2014, McGill *et al*., 2015), particularly for plants in which the paucity of long-term field data and complexity of biodiversity hampers substantial empirical validation (Feeley *et al*., 2012). Despite limitations inherent to estimating species niches and distributions with correlative methods (Thuiller *et al*., 2008; Peterson *et al*., 2011), this approach allows inference to be made about species climatic suitability over larger spatial and temporal scales given the scarcity of observational data. Here we have used a comprehensive database of carefully built ecological niche models for 2,255 species native to the Atlantic Forest to infer about future biodiversity changes in one the most important world's hostspot for conservation (Mittermeier *et al.*, 2011). We clearly show that in spite of increases or invariability of species richness, the Atlantic Forest will likely experience compositional turnover leading to biotic homogenization across space and over time. Furthermore, our results enabled us to depict complementing aspects of biodiversity based on solid mathematical and statistical inference, demonstrating mechanisms by which diversity may be threatened under climate change. We highlight the urgency of mitigation actions and suggest conservation efforts to focus on narrowly distributed species as they constribute most to beta diversity.

Acknowledgments

We are grateful to Narayani Barve for assistance with R scripts and A. Townsend Peterson for discussions and guidance during niche modeling. V. P. Z. recieved Ph.D. scholarship from the 'Coordenação de Aperfeiçoamento de Pessoal de Nível Superior' during this research.

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Tables

Table 1. Summary of diversity metrics of the entire woody plant assemblage in the Atlantic Forest for projections based on present and future climatic scenarios. Whittaker's beta diversity (beta) is given by the total number of species (S=2255) or total number of sites (N=14905) divided by the average local richness and range size, respectively. Percentages represent the average number of species in each site and the average number of sites that each species occupies.

Scenario	Beta	average richness	average range size	% species-sites
Present	2.99	753.41	4979.89	33.41
2650	2.82	799.03	5281.40	35.43
2670	2.79	807.41	5336.80	35.81
8550	2.76	816.13	5394.44	36.19
8570	2.64	854.43	5647.56	37.89

Low greenhouse gas emissions scenario in 2050= 2650; Low greenhouse gas emissions scenario in 2070=2670; high greenhouse gas emissions scenario in 2050=8550; high greenhouse gas emissions scenario in 2070=8570

Figure captions

Fig. 1 Per-site Range-diversity plot of current woody plant assemblages in the Atlantic forest and geographic associations of high richness-and-small ranges quartile (upper left) and low richness-and-large ranges quartile (lower right).

Fig. 2 Per-site Range-diversity plot of current woody plant assemblages in the Atlantic forest and corresponding ecorregions

Fig. 3 Per-site Range-diversity plot of current woody plant assemblages in the Atlantic forest and projected beta diversity and maximum covariance lines for assemblages under different climate change scenarios (Low greenhouse gas emissions scenario in 2050= 2650, Low greenhouse gas emissions scenario in 2070=2670, high greenhouse gas emissions scenario in 2050=8550, high greenhouse gas emissions scenario in 2070=8570).

Fig. 4 Means (circles) and standard deviation (horizontal bars) of proportional richness, mean proportional range size and covariance for different Atlantic forest ecoregions under current climatic conditions and different climate change scenarios (Low greenhouse gas emissions scenario in 2050= 2650, Low greenhouse gas emissions scenario in 2070=2670, high greenhouse gas emissions scenario in 2050=8550, high greenhouse gas emissions scenario in 2070=8570).

Fig. 5 Proportional species richness, mean proportional range size and covariance differences among woody plant species assemblages within strict protected areas under current climatic conditions and different climate change scenarios (Low greenhouse gas emissions scenario in 2050= 2650, Low greenhouse gas emissions scenario in 2070=2670, high greenhouse gas emissions scenario in 2050=8550, high greenhouse gas emissions scenario in 2070=8570).

Figures

Fig. 1

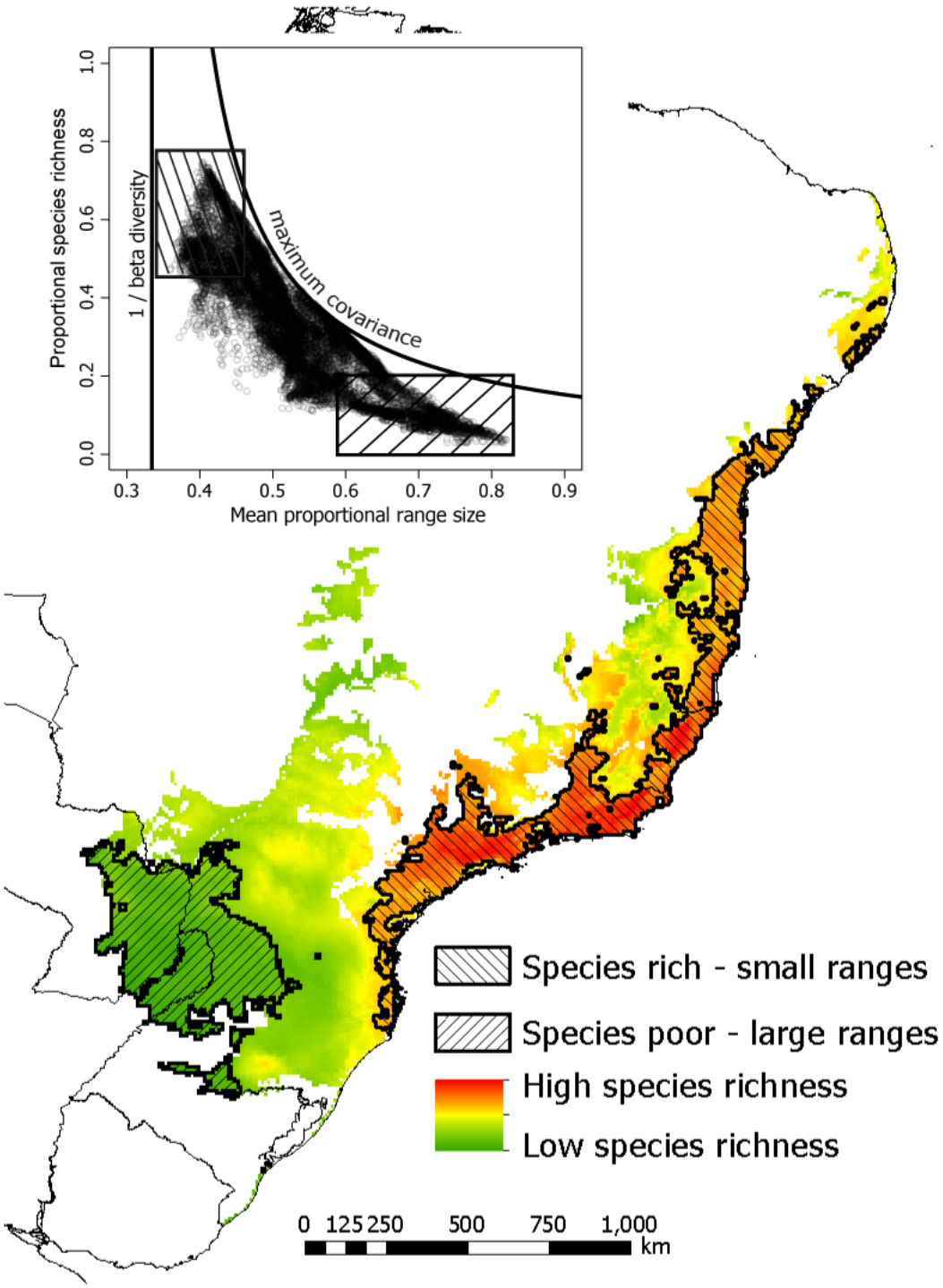


Fig. 2

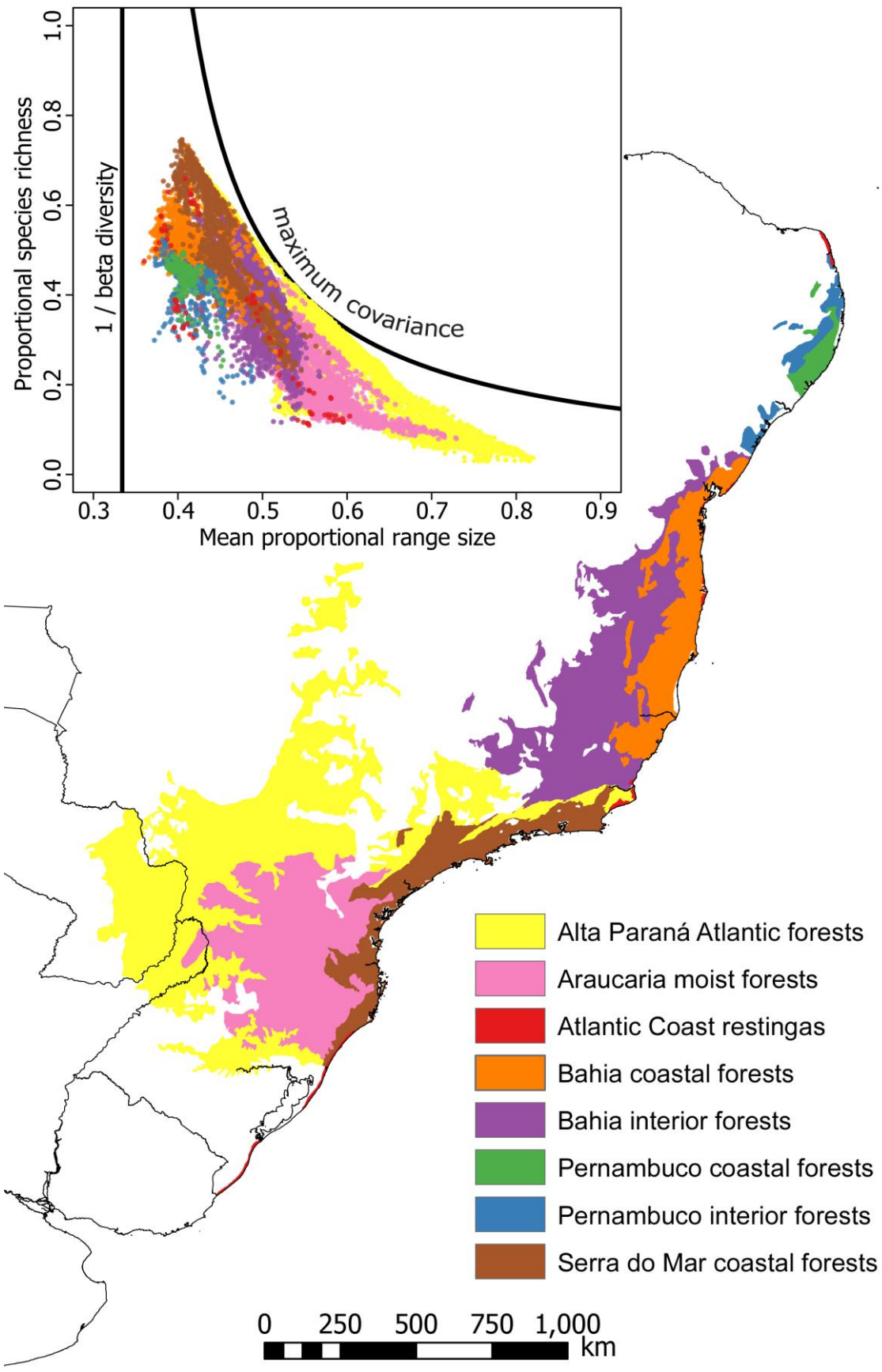

Proportional species richness
0.0
0.2
0.4
0.6
0.8
1.0
1 / beta diversity
maximum covariance
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Mean proportional range size
Alta Paraná Atlantic forests
Araucaria moist forests
Atlantic Coast restingas
Bahia coastal forests
Bahia interior forests
Pernambuco coastal forests
Pernambuco interior forests
Serra do Mar coastal forests
0
250
500
750
1,000
km

Fig. 3

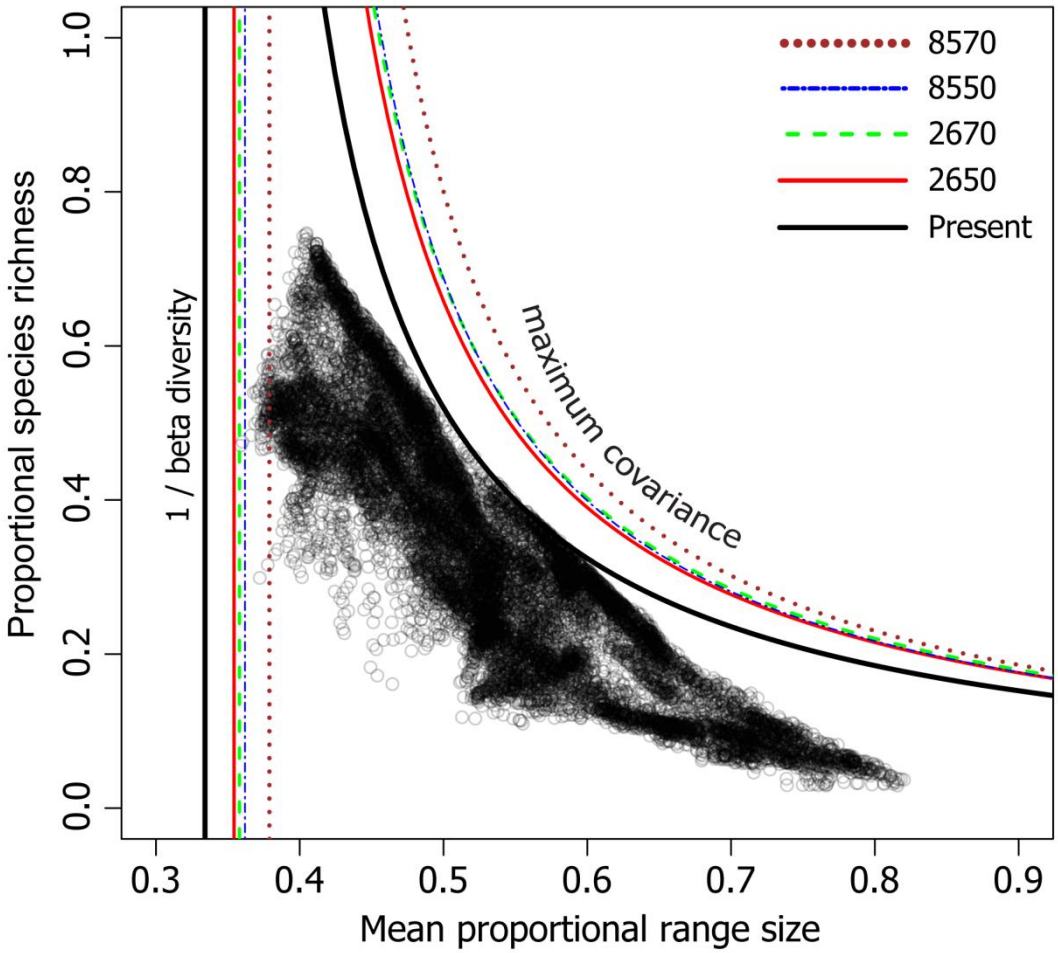

8570
8550
2670
2650
Present
maximum covariance
1 / beta diversity
Proportional species richness
0.0
0.2
0.4
0.6
0.8
1.0
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Mean proportional range size

Fig. 4

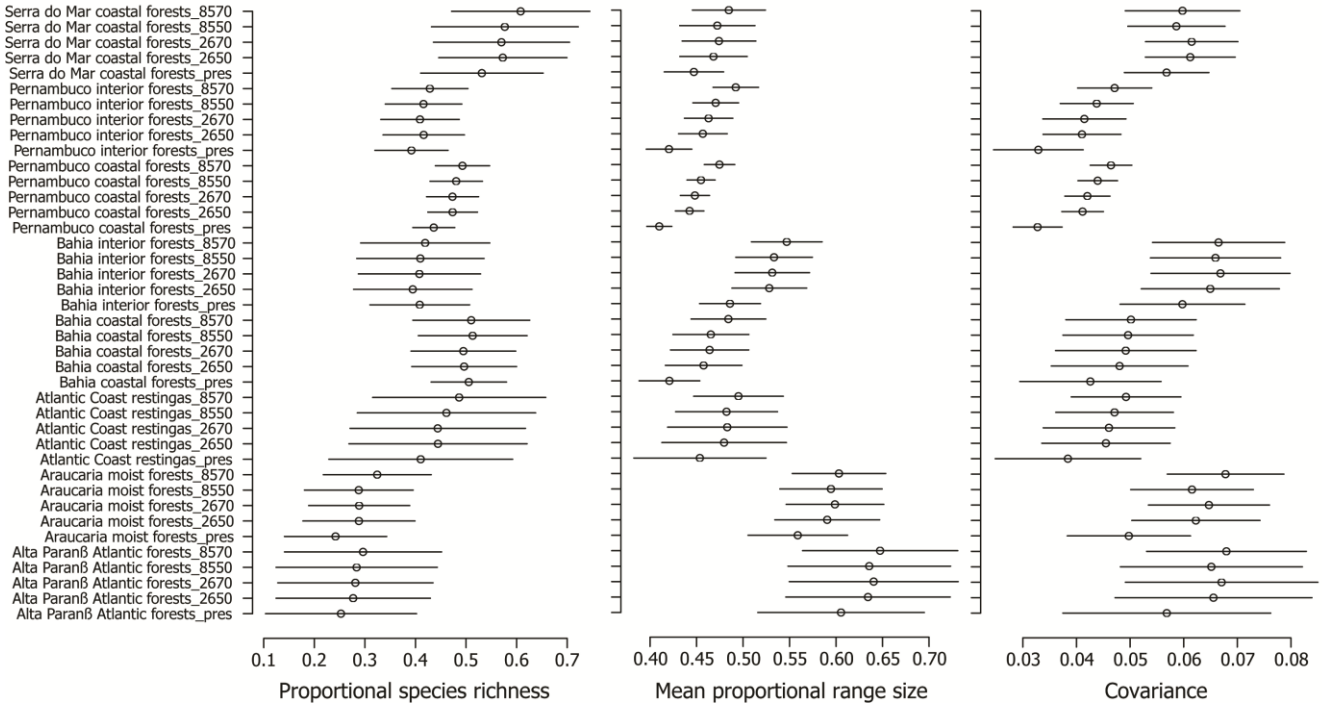
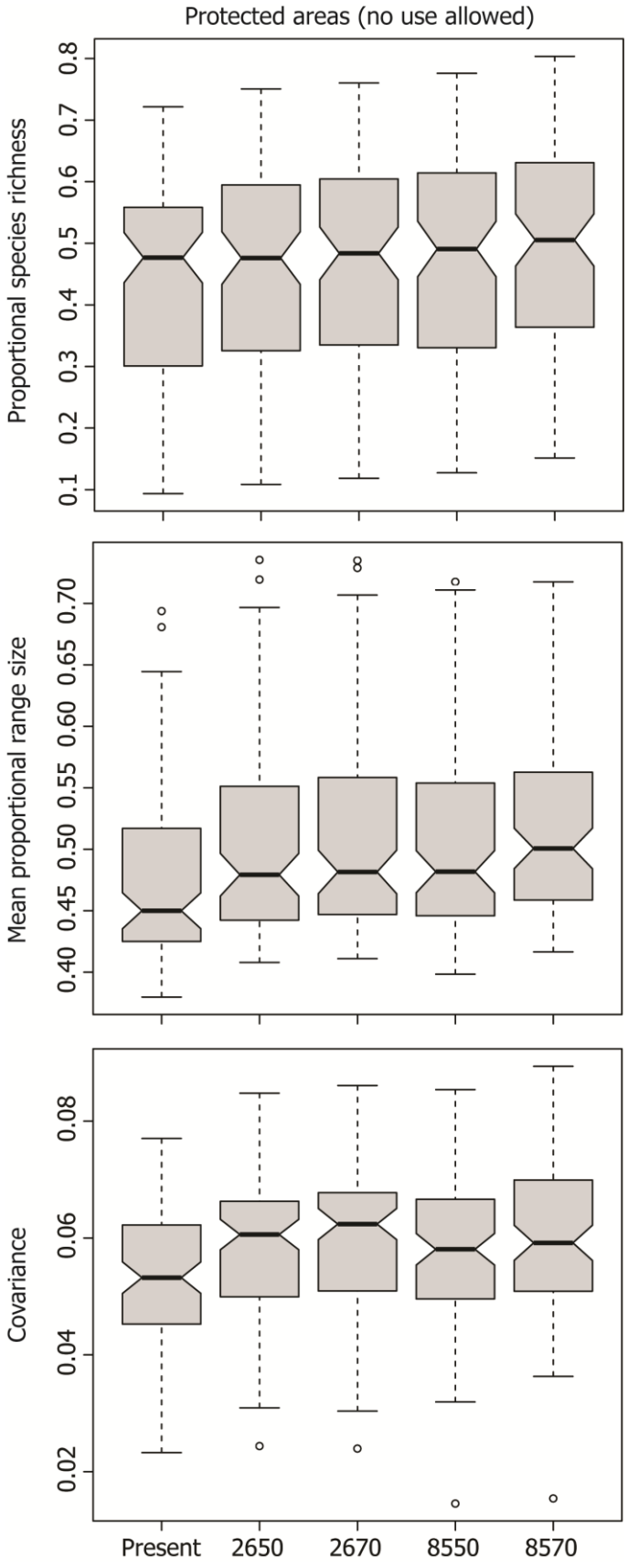

Serra do Mar coastal forests_8570
Serra do Mar coastal forests_8550
Serra do Mar coastal forests_2670
Serra do Mar coastal forests_2650
Serra do Mar coastal forests_pres
Pernambuco interior forests_8570
Pernambuco interior forests_8550
Pernambuco interior forests_2670
Pernambuco interior forests_2650
Pernambuco interior forests_pres
Pernambuco coastal forests_8570
Pernambuco coastal forests_8550
Pernambuco coastal forests_2670
Pernambuco coastal forests_2650
Pernambuco coastal forests_pres
Bahia interior forests_8570
Bahia interior forests_8550
Bahia interior forests_2670
Bahia interior forests_2650
Bahia interior forests_pres
Bahia coastal forests_8570
Bahia coastal forests_8550
Bahia coastal forests_2670
Bahia coastal forests_2650
Bahia coastal forests_pres
Atlantic Coast restingas_8570
Atlantic Coast restingas_8550
Atlantic Coast restingas_2670
Atlantic Coast restingas_2650
Atlantic Coast restingas_pres
Araucaria moist forests_8570
Araucaria moist forests_8550
Araucaria moist forests_2670
Araucaria moist forests_2650
Araucaria moist forests_pres
Alta Paranß Atlantic forests_8570
Alta Paranß Atlantic forests_8550
Alta Paranß Atlantic forests_2670
Alta Paranß Atlantic forests_2650
Alta Paranß Atlantic forests_pres
0.1 0.2 0.3 0.4 0.5 0.6 0.7
Proportional species richness
0.40 0.45 0.50 0.55 0.60 0.65 0.70
Mean proportional range size
0.03 0.04 0.05 0.06 0.07 0.08
Covariance

Fig. 5


Protected areas (no use allowed)
Proportional species richness
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Mean proportional range size
0.40
0.45
0.50
0.55
0.60
0.65
0.70
Covariance
0.02
0.04
0.06
0.08
Present
2650
2670
8550
8570

5 CONCLUSÕES

A Mata Atlântica apresenta extraordinária biodiversidade resultante de uma combinação de fatores agindo em diferentes escalas espaciais e temporais. Em larga escala, condições climáticas atuais e fatores históricos e intrínsecos, estruturados no espaço, possuem grande importância como determinantes da riqueza e composição de metacomunidades de plantas lenhosas. Dentre os principais fatores climáticos atuais estão variáveis relacionadas à produtividade do ambiente e tolerância a extremos de temperatura, dando suporte à teoria energética e de tolerância a condições abióticas. Variáveis do solo relacionadas aos recursos utilizados por plantas, apesar de serem localmente importantes, não apresentaram grande importância em larga escala, corroborando a ideia de que interações entre organismos e competição por recursos tende a ser mais importante em escalas locais. Um conjunto semelhante de variáveis ambientais explica a composição de espécies e propriedades coletivas (riqueza) de metacomunities de plantas lenhosas na Mata Atlântica. Os resultados obtidos no primeiro capítulo salientam a importância de se investigar padrões de diversidade sob diferentes perspectivas e teorias para se adquirir melhor entendimento dos mecanismos que promovem diversidade.

A Mata Atlântica está extremamente ameaçada pela redução e modificação de hábitat que em sinergia com mudanças climáticas podem compromenter a persistência de espécies vegetais. Considerando que o clima é um fator determinante da distribuição de espécies em larga escala (capítulo 1), foram gerados mapas de distribuição potencial de plantas lenhosas com base em variáveis climáticas e comparados diferentes cenários de manejo. Os resultados do segundo capítulo demonstram que ações de conservação envolvendo a proteção dos remanescentes em conjunto com restauração de áreas degradadas são urgentemente necessárias para reverter a atual crise de biodiversidade. Estas ações, se implementadas de forma planejada e considerando diferentes fatores socioeconômicos, podem maximizar a conservação de espécies reduzindo custos e conflitos com urbanização e atividades agropecuárias.

Mudanças no clima podem causar alterações na distribuição de espécies, um efeito menos evidente e estudado são alterações em padrões de diversidade decorrente de respostas individualizadas das espécies. A expansão de espécies generalistas tolerantes a alterações climáticas e retração de espécies endêmicas vulneráveis pode levar a redução da diversidade beta no decorrer do tempo. No terceiro capítulo este mecanismo é evidenciado. Espécies amplamente distribuídas na Mata Atlântica apresentaram tendência de expanção dos limites de distribuição, levando a um aumento da riqueza na escala local e diminuição da diversidade beta na escala regional em diferentes cenários de mudanças climáticas. Os resultados do terceiro capítulo alertam sobre o provável efeito de mudanças climáticas na reorganização de comunidades que pode potencializar homogenização biótica e ameaçar a preservação da biodiversidade na Mata Atlântica.

6 ANEXOS

6.1 Capítulo 1 **Supplementary material**

Appendix A1 Compiled plant survey studies in the Atlantic Forest in increasing order of latitude (North-South).

Site	Reference	Municipality	State	Method	Longitude	Latitude	Richness	N^{o} of trees	Total area sampled
1	Trindade 1991	Natal	RN	floristic	35W 12'	5S 48'	38	-	-
2	Cestaro & Soares 2004	Macaíba	RN	pc-quarter	35W 22'	5S 52'	51	800	-
3	Cestaro & Soares 2008	Parnamirim	RN	plot/floristic	35W 10'	5S 55'	57	-	-
4	Almeida Jr et al. 2009	Tibau do Sul	RN	floristic	35W 13'	6S 13'	56	-	-
5	Oliveira-Filho & Carvalho 1993	Mataraca	PB	floristic	34W 58'	6S 28'	130	-	-
6	Xavier 2009*	Dona Inês	PB	pc-quarter	35W 36'	6S 37'	44	520	0.35
7	Xavier 2009*	Dona Inês	PB	pc-quarter	35W 37'	6S 37'	38	520	0.37
8	Barbosa et al. 2011	Mamanguape	PB	floristic	35W 12'	6S 40'	180	-	-
9	Pereira & Alves 2006	Lucena	PB	floristic	34W 55'	6S 51'	65	-	-
10	Santos et al. 2010*	Cruz do Espírito Santo	PB	plot	35W 07'	6S 58'	48	1122	0.15
11	Oliveira et al. 2006*	Areia	PB	plot	35W 42'	6S 58'	73	4997	0.76
12	Barbosa 1996*	João Pessoa	PB	plot/floristic	34W 52'	7S 06'	57/136	1102	1
13	Amazonas & Barbosa 2011	João Pessoa	PB	floristic	34W 51'	7S 07'	82	-	-
14	Vitória 2009*	Itambé	PE	plot	35W 10'	7S 25'	34	580	0.5

15	Oliveira 2006*	Timbaúba	PE	plot	35W 22'	7S 25'	42	235	0.26
16	Oliveira 2006*	Aliança	PE	plot	35W 09'	7S 28'	37	212	0.26
17	Pontes & Barbosa 2008	Cabedelo	PB	floristic	34W 51'	7S 30'	62	-	-
18	Vitória 2009*	Itambé	PE	plot	35W 10'	7S 30'	30	577	0.5
19	Lopes 2007*	São Vicente Férrer	PE	plot	35W 28'	7S 37'	88	1390	1
20	Ferraz & Rodal 2006*	São Vicente Férrer	PE	plot/floristic	35W 30'	7S 37'	112/209	1521	1
21	Lopes 2007*	Aliança	PE	plot	35W 15'	7S 40'	54	649	1
22	Holanda 2008*/ Oliveira 2006	Nazaré da Mata	PE	plot	35W 12'	7S 43'	55	1086	1
23	Rocha 2007*	Igarassu	PE	plot	34W 58'	7S 49'	84	1306	1
24	Brandão et al. 2009	Igarassu	PE	plot	35W 00'	7S 49'	76	1672	1
25	Pessoa et al. 2009	Paulista	PE	floristic	34W 55'	7S 55'	106	-	-
26	Guedes 1992	Recife	PE	floristic	34W 55'	8S 00'	73	-	-
27	Oliveira 2011*	São Lourenço da Mata	PE	plot/floristic	35W 10'	8S 01'	38	1025	0.37
28	Andrade & Rodal 2004*	São Lourenço da Mata	PE	plot	35W 09'	8S 03'	69	1145	1
29	Souza Jr 2006*	Recife	PE	plot	34W 55'	8S 04'	72	1003	1
30	Alves Junior et al. 2006*	Recife	PE	plot	34W 57'	8S 04'	54	531	0.5
31	Feitosa 2004*	Recife	PE	plot	34W 57'	8S 06'	40	1586	1
32	Oliveira 2011*	Moreno	PE	plot/floristic	35W 07'	8S 06'	56	851	0.37
33	Silva Jr 2004*	Cabo de Santo Agostinho	PE	plot	35W 01'	8S 10'	93	1166	1

34	Nascimento 2001*	Brejo da Madre de Deus	PE	plot	36W 22'	8S 10'	47	1391	1
35	Pôrto et al. 2005	Gurjáu	PE	plot	35W 28'	8S 13'	79	-	0.4
36	Siqueira 1997*	Cabo de Santo Agostinho	PE	plot/floristic	34W 58'	8S 18'	60/71	1405	1
37	Tavares 1998*	Caruaru	PE	plot	36W 00'	8S 18'	60	956	1
38	Correia 1996	Pesqueira	PE	plot/floristic	36W 46'	8S 19'	51	-	-
39	Oliveira 2003	Ibateguara	AL	floristic	35W 49'	8S 30'	109	-	-
40	Silva 2009*	Sirinhaém	PE	plot	35W 10'	8S 34'	86	1542	1.5
41	Costa Jr et al. 2008*	Catende	PE	plot	35W 40'	8S 37'	78	992	1
42	Guimarães 2005	Catende	PE	plot	35W 34'	8S 40'	44	1076	0.35
43	Teixeira 2009*	Tamandaré	PE	plot	35W 10'	8S 43'	77	1484	1.05
44	Costa Jr et al. 2007	Catende	PE	plot	35W 37'	8S 43'	76	1049	1
45	Pôrto et al. 2005	Frei Caneca	PE	plot	35W 49'	8S 43'	119	-	0.4
46	Silva et al. 2008	Tamandaré	PE	floristic	35W 06'	8S 46'	50	-	-
47	Pôrto et al. 2005	Serra Grande	AL	plot	35W 49'	8S 58'	103	-	0.4
48	Medonça 2005	Murici	AL	plot/floristic	35W 52'	9S 12'	112/135	2292	1.05
49	Vicente 1999	Itabaiana	SE	floristic	37W 25'	10S 40'	80	-	-
50	Oliveira et al. 2012*	Salgado	SE	circular plot	37W 28'	10S 40'	71	1874	0.79
51	Menezes et al. 2012	Mata de São João	BA	plot	37W 58'	12S 31'	28	1640	0.2
52	Sobrinho & Queiroz 2005	Santa Terezinha	BA	floristic	39W 28'	12S 51'	97	-	-

53	Costa & Guedes 2010	Elísio Medrado	BA	floristic	39W 31'	12S 56'	52	-	-
54	Costa & Guedes 2010	Amargosa	BA	floristic	39W 36'	13S 01'	43	-	-
55	Martini et al. 2007*	Uruçuca	BA	pc-quarter	39W 03'	14S 21'	137	203	0.1
56	Martini et al. 2007*	Uruçuca	BA	pc-quarter	39W 04'	14S 22'	134	210	0.1
57	Thomas et al. 2008*	Uruçuca	BA	transect	39W 01'	14S 24'	208	2530	1
58	Martini et al. 2007*	Uruçuca	BA	pc-quarter	39W 06'	14S 28'	144	200	0.1
59	Sambuichi 2002	Ilhéus	BA	plot	39W 15'	14S 36'	30	138	2.6
60	Sambuichi 2006	Ilhéus	BA	plot	39W 09'	14S 43'	47	120	1.7
61	Amorim et al. 2009	Barro Preto	BA	floristic	39W 31'	14S 46'	172	-	-
62	Amorim et al. 2008	Una	BA	floristic	39W 03'	15S 10'	447	-	-
63	Amorim et al. 2009	Arataca	BA	floristic	39W 19'	15S 10'	280	-	-
64	Thomas et al. 2009*/Amorim et al. 2005	Jussari	BA	plot/floristic	39W 28'	15S 12'	166/281	1098	1
65	Oliveira-Filho & Ratter 1994	Ilhéus	BA	floristic	39W 10'	15S 19'	439	-	-
66	Rocha & Amorim 2012	Camacan	BA	floristic	39W 33'	15S 22'	357	-	-
67	Rocha & Amorim 2012*	Camacan	BA	plot	39W 34'	15S 22'	221	1604	0.5
68	Amorim et al. 2009	Camacan	BA	floristic	39W 34'	15S 23'	223	-	-
69	Carvalho 2011*	Porto Seguro	BA	plot	39W 04'	16S 16'	243	1810	1
70	Oliveira -Filho et al. 2005	Virgem da Lapa	MG	floristic	42W 13'	16S 43'	147	-	-
71	Oliveira -Filho et al. 2005	Posses	MG	floristic	42W 46'	16S 54'	229	-	-

72	Oliveira -Filho et al. 2005	Leme do Prado	MG	floristic	42W 43'	17S 04'	237	-	-
73	Oliveira -Filho et al. 2005	Machacalis	MG	floristic	40W 34'	17S 10'	207	-	-
74	Oliveira -Filho et al. 2005	Chapada de São Domingos	MG	floristic	43W 07'	17S 28'	206	-	-
75	Pereira & Gomes 1994	Conceição da Barra	ES	floristic	39W 52'	18S 10'	103	-	-
76	Oliveira -Filho et al. 2005	São Pedro do Suaçuí	MG	floristic	42W 36'	18S 22'	165	-	-
77	Oliveira -Filho et al. 2005	Governador Valadares	MG	floristic	42W 01'	18S 51'	167	-	-
78	Simonelli et al. 2008*	Linhares	ES	plot	39W 53'	19S 04'	60	1399	1
79	Oliveira -Filho et al. 2005	Braúnas/Joanésia	MG	floristic	42W 43'	19S 09'	186	-	-
80	Oliveira-Filho & Ratter 1994	Linhares	ES	floristic	40W 04'	19S 18'	105	-	-
81	Pereira et al. 1998	Linhares	ES	floristic	40W 05'	19S 20'	91	-	-
82	Oliveira -Filho et al. 2005	Itambé do Mato Dentro	MG	floristic	43W 13'	19S 25'	210	-	-
83	Oliveira -Filho et al. 2005	Aimorés	MG	floristic	41W 04'	19S 28'	204	-	-
84	Oliveira-Filho & Ratter 1994	Timóteo	MG	floristic	42W 34'	19S 40'	134	-	-
85	Oliveira -Filho et al. 2005	Santa Barbara	MG	floristic	43W 22'	19S 54'	173	-	-
86	Saiter 2007	Santa Teresa	ES	plot	40W 31'	19S 57'	325	-	1.02
87	Pereira et al. 2000	Serra	ES	floristic	40W 10'	20S 05'	51	-	-
88	Magnago et al. 2011*	Serra	ES	plot	40W 13'	20S 09'	66	851	0.6
89	Leite et al. 2007	Serra	ES	floristic	40W 19'	20S 10'	70	-	-
90	Pereira & Assis 2000	Vitoria	ES	floristic	40W 15'	20S 14'	52	-	-

91	Oliveira -Filho et al. 2005	Rio Doce	MG	floristic	42W 54'	20S 15'	321	-	-
92	Oliveira -Filho et al. 2005	Mariana	MG	floristic	43W 10'	20S 22'	296	-	-
93	Reis et al. 2007	Diogo de Vasconcelos	MG	plot	43W 10'	20S 25'	150	-	2
94	Pereira & Zambom 1998	Vila Velha	ES	floristic	40W 20'	20S 27'	79	-	-
95	Reis et al. 2007	Piranga	MG	plot	43W 16'	20S 33'	212	-	2
96	Fabris & Cesar 1996	Guarapari	ES	plot	40W 25'	20S 34'	70	-	0.5
97	Assis et al. 2004a,b	Guarapari	ES	plot	40W 25'	20S 36'	84	2106	1
98	Oliveira -Filho et al. 2005	Castelo	ES	floristic	41W 10'	20S 37'	282	-	-
99	Reis et al. 2007	Piranga	MG	plot	43W 22'	20S 37'	139	-	1.4
100	Reis et al. 2007	Piranga	MG	plot	43W 19'	20S 40'	161	-	2.2
101	Soares 2005*	Araponga	MG	pc-quarter	42W 29'	20S 41'	125	600	0.34
102	Oliveira -Filho et al. 2005	Carangola	MG	floristic	42W 01'	20S 43'	283	-	-
103	Ferreira Jr. 2005*	Viçosa	MG	plot	42W 45'	20S 45'	121	1371	1
104	Santos 2005*	Viçosa	MG	plot	42W 55'	20S 45'	123	808	0.5
105	Oliveira-Filho & Ratter 1994	Tiradentes	MG	floristic	44W 13'	21S 01'	250	-	-
106	Silva et al. 2003*	Ibituruna	MG	plot	44W 49'	21S 09'	110	1008	1.04
107	Oliveira-Filho & Ratter 1994	Bom Sucesso	MG	floristic	44W 54'	21S 09'	220	-	-
108	Rocha et al. 2005*	Coqueiral	MG	plot/floristic	45W 28'	21S 09'	158/230	1475	1
109	Oliveira-Filho et al. 1994/Oliveira-Filho & Ratter 1994	Lavras	MG	plot/floristic	44W 57'	21S 13'	131/180	6527	5.04

110	Souza et al. 2003*	Lavras	MG	plot/floristic	44W 22'	21S 18'	136/161	1666	1.12
111	Dalanesi et al. 2004*	Lavras	MG	plot/floristic	44W 58'	21S 19'	203/368	4137	2.4
112	Oliveira-Filho & Ratter 1994	Lavras	MG	floristic	45W 00'	21S 19'	192	-	-
113	Oliveira-Filho & Ratter 1994	Itutinga	MG	floristic	44W 37'	21S 22'	224	-	-
114	Silva & Nascimento 2001 /Nascimento & Lima 2008	São Francisco do Itabapoana	RJ	plot/floristic	41W 04'	21S 24'	149	-	1
115	Botrel et al. 2002*	Ingaí	MG	plot/floristic	44W 55'	21S 24'	135/203	2683	1
116	Carvalho et al. 2007*	Piedade do Rio Grande	MG	plot/floristic	44W 06'	21S 28'	171/268	1782	1.2
117	Oliveira-Filho & Ratter 1994	Madre de Deus de Minas	MG	floristic	44W 22'	21S 28'	173	-	-
118	Rodrigues et al. 2002*	Luminárias	MG	plot/floristic	44W 55'	21S 28'	155/193	2343	1.28
119	Oliveira -Filho et al. 2005	Miraí	MG	floristic	42W 36'	21S 31'	269	-	-
120	Carvalho et al. 2006	C. Goytacazes	RJ	pc-quarter	41W 15'	21S 42'	88	336	-
121	Carvalho et al. 2000	Ibitipoca	MG	plot	43W 52'	21S 42'	108	1912	0.64
122	Assumpção & Nascimento 2000	S. J. da Barra	RJ	plot	41W 02'	21S 43'	39	-	0.09
123	Moreno et al. 2003	C. Goytacazes	RJ	plot	41W 19'	21S 48'	106	480	0.6
124	Silva & Soares 2002*	São Carlos	SP	plot	47W 48'	21S 55'	64	1239	1
125	Valente et al. 2011	Rio Preto	MG	plot	43W 52'	21S 58'	117	880	0.25
126	Valente et al. 2011	Rio Preto	MG	plot	43W 52'	21S 58'	77	806	0.25
127	Valente et al. 2011	Rio Preto	MG	plot	43W 52'	22S 00'	24	698	0.25
128	Pereira et al. 2005	Aiuruoca	MG	floristic	44W 36'	22S 01'	226	-	-

129	Silva et al. 2009*	São Sebastião da Bela Vista	MG	plot/floristic	45W 48'	22S 06'	49/78	2064	1.08
130	Pereira et al. 2005	Bocaina de Minas	MG	floristic	44W 28'	22S 10'	78	-	-
131	Pereira et al. 2005	Bocaina de Minas	MG	floristic	44W 31'	22S 13'	210	-	-
132	Pereira et al. 2005	Bocaina de Minas	MG	floristic	44W 34'	22S 13'	118	-	-
133	Montezuma & Araújo 2007	Carapebus	RJ	plot	41W 40'	22S 15'	33	3522	1
134	Pereira et al. 2005	Visconde de Mauá	RJ	floristic	44W 36'	22S 19'	185	-	-
135	Oliveira-Filho & Ratter 1994	Bauru	SP	floristic	49W 04'	22S 19'	94	-	-
136	Oliveira-Filho & Ratter 1994	Ipeúna	SP	floristic	48W 45'	22S 25'	192	-	-
137	Kurtz & Araújo 2000*	C. de Macacu	RJ	pc-quarter	42W 52'	22S 28'	114	592	0.44
138	Borém et al. 2002	Silva Jardim	RJ	plot	42W 31'	22S 30'	146	579	0.36
139	Guedes-Bruni et al. 2006	Silva Jardim	RJ	plot	42W 15'	22S 31'	82	-	1
140	Pessoa & Oliveira 2006	Silva Jardim	RJ	plot	42W 16'	22S 31'	100	-	0.65
141	Christo et al. 2009*	Silva Jardim	RJ	plot	42W 19'	22S 31'	102	734	0.5
142	Barroso 2009	Teresópolis	RJ	plot	42W 58'	22S 31'	123	1274	0.3
143	Carvalho et al. 2006 b	Silva Jardim	RJ	plot	42W 15'	22S 32'	25	628	0.72
144	Carvalho et al. 2010	Silva Jardim	RJ	plot	42W 17'	22S 33'	29	628	0.72
145	Souza et al. 2007*	Volta Redonda	RJ	plot	44W 04'	22S 33'	129	968	0.3
146	Sobrinho et al. 2008*	Nova Iguaçu	RJ	plot	43W 24'	22S 34'	44	251	0.2
147	Del Quiqui et al. 2007*	Diamante do Norte	PR	plot/floristic	52W 49'	22S 34'	99/109	3808	4.35

148	Giovanetti Alves et al. 2010	Piraí	RJ	plot	43W 53'	22S 37'	98	1211	0.4
149	Oliveira-Filho & Ratter 1994	Anhembi	SP	floristic	48W 10'	22S 40'	123	-	-
150	Costa Filho et al. 2006*	Diamante do Norte	PR	plot	52W 55'	22S 40'	92	2450	1.5
151	Carvalho et al. 2007*	Rio Bonito	RJ	plot	42W 37'	22S 42'	86	698	0.4
152	Lobão & Kurtz 2000	Armacão de Buzios	RJ	plot	41W 52'	22S 45'	24	312	0.1
153	Gandra et al. 2011*	Itaguaí	RJ	plot	43W 49'	22S 48'	75	943	0.5
154	Gomes et al. 2004*	Pindamonhangaba	SP	plot	45W 31'	22S 48'	68	517	0.25
155	Santos & Kinoshita 2003	Campinas	SP	floristic	46W 55'	22S 50'	162	-	-
156	Sá 1992	Saquarema	RJ	floristic	42W 31'	22S 52'	102	-	-
157	Pereira et al. 2001	Maricá	RJ	line intercept transect	42W 49'	22S 52'	35	398	-
158	Lemos et al. 2001	Maricá	RJ	plot	42W 49'	22S 55'	43	276	0.02
159	Peixoto et al. 2004	Rio de Janeiro	RJ	pc-quarter	43W 37'	22S 56'	61	-	-
160	Dias 2005	Rio de Janeiro	RJ	line intercept transect	43W 36'	23S 01'	61	1938	-
161	Oliveira 2002	Angra dos Reis	RJ	plot	44W 10'	23S 07'	100	519	0.26
162	Araújo et al. 1997	Angra dos Reis	RJ	plot	44W 16'	23S 10'	41	-	0.75
163	Oliveira-Filho & Ratter 1994	Atibaia	SP	floristic	46W 25'	23S 10'	198	-	-
164	Cotarelli et al. 2008	Londrina	PR	floristic	51W 00'	23S 15'	176	-	-
165	Padgurschi et al. 2011*	São Luiz do Paraitinga	SP	plot	45W 03'	23S 16'	147	1852	1

166	Ivanauskas et al. 1999*	Itatinga	SP	plot	48W 33'	23S 16'	83	845	0.42
167	Assis et al. 2011*	Ubatuba	SP	plot	44W 46'	23S 19'	82	1664	1
168	Campos et al. 2011*	Ubatuba	SP	plot	44W 49'	23S 19'	134	1274	1
169	Lacerda 2001	Ubatuba	SP	plot	44W 46'	23S 20'	77	-	0.18
170	Lacerda 2001	Ubatuba	SP	plot	44W 47'	23S 21'	96	-	0.18
171	Assis 1999	Ubatuba	SP	plot	44W 50'	23S 21'	48	152	0.1
172	Rochelle et al. 2011*	Ubatuba	SP	plot	45W 04'	23S 21'	177	1881	1
173	Sanches et al. (1998)	Ubatuba	SP	plot	44W 48'	23S 22'	114	673	0.4
174	Cesar & Monteiro 1995*	Picinguaba	SP	plot	44W 50'	23S 22'	44	908	0.52
175	Assis et al. 2011*	Ubatuba	SP	plot	44W 51'	23S 22'	135	1078	1
176	Gomes et al. 2011*	Ubatuba	SP	plot	45W 04'	23S 22'	146	1496	1
177	Gomes et al. 2011*	Ubatuba	SP	plot	45W 04'	23S 22'	184	1993	1
178	Padgurschi et al. 2011*	São Luiz do Paraitinga	SP	plot	45W 10'	23S 24'	121	1436	1
179	Bianchini et al. 2003*/Rossetto & Vleira 2010	Londrina	PR	plot/floristic	51W 15'	23S 27'	60/248	904	0.5
180	Reis-Duarte 2004	Ubatuba	SP	plot	45W 05'	23S 29'	34	3585	0.7
181	Dilish 2002	São Paulo	SP	plot	46W 43'	23S 33'	86	934	2
182	Bernacci et al. 2006	Cotia	SP	pc-quarter	46W 52'	23S 37'	327	7400	-
183	Catharino et al. 2006*	Cotia	SP	pc-quarter	47W 01'	23S 39'	235	2400	-
184	Guedes et al. 2006	Bertioga	SP	plot	46W 07'	23S 49'	57	476	0.48

185	Guedes et al. 2006	Bertioga	SP	plot	46W 07'	23S 49'	61	417	0.48
186	Guilherme et al. 2004*	Sete Barras	SP	plot	48W 04'	24S 13'	242	3078	-
187	Oliveira et al. 2001*	Peruíbe	SP	plot	47W 00'	24S 16'	44	284	0.2
188	Carvalhaes 1997	Iguape	SP	plot	47W 15'	24S 25'	31	-	0.1
189	Melo et al. 2000*	Peruíbe	SP	plot	47W 15'	24S 30'	158	1785	1
190	Aidar et al. 2001*	Iporanga	SP	plot	48W 40'	24S 31'	87	445	0.3
191	Cardoso-Leite et al. 2013*	Barra do Turvo	SP	plot	48W 22'	24S 33'	130	1501	0.8
192	Ivanauskas 1997*	Pariquera-Açu	SP	plot	47W 52'	24S 36'	158	1956	1.21
193	Torezan 1995	Iporanga	SP	plot	48W 37'	24S 36'	90	-	0.1
194	Sztutman & Rodrigues 2002*	Pariquera-Açu	SP	plot	47W 48'	24S 40'	106	747	0.54
195	Silva 2006	Ilha Comprida	SP	plot	47W 45'	24S 53'	38	2253	0.5
196	Silva 2006	Ilha Comprida	SP	plot	47W 46'	24S 54'	37	2253	0.5
197	Urbanetz et al. 2010	Cananéia	SP	floristic	47W 55'	24S 54'	206	-	-
198	Scheer et al. 2011*	Campina Grande do Sul	PR	plot	48W 12'	24S 55'	26	549	0.12
199	Scheer et al. 2011*	Guaraqueçaba	PR	plot	48W 09'	24S 58'	34	746	0.12
200	Melo & Mantovani 1994	Cananéia	SP	plot	47W 53'	25S 02'	129	-	1
201	Galvão et al. 2002	Guaraqueçaba	PR	plot	48W 12'	25S 06'	12	299	0.16
202	Zacarias 2008*	Guaraqueçaba	PR	plot	48W 27'	25S 09'	77	395	0.16
203	Sugiyama 1998	Cananéia	SP	plot	47W 58'	25S 10'	63	-	0.37

204	Liebsch et al. 2007/Borgo et al. 2011*	Antonina	PR	plot/floristic	48W 42'	25S 19'	90/333	863	0.4
205	Koehler et al. 2002	Morretes	PR	plot	48W 54'	25S 21'	18	-	0.05
206	Koehler et al. 2002	Quatro Barras	PR	plot	48W 58'	25S 22'	27	-	0.05
207	Portes et al. 2001	Quatro Barras	PR	plot	49W 00'	25S 23'	25	449	0.1
208	Rocha 1999	Morretes	PR	plot	48W 45'	25S 24'	27	321	0.8
209	Jaster 1995	Guaraqueçaba	PR	plot	48W 12'	25S 25'	46	-	0.81
210	Jaster 1995	Guaraqueçaba	PR	plot	48W 13'	25S 25'	62	-	0.45
211	Jaster 1995	Guaraqueçaba	PR	plot	48W 13'	25S 25'	78	-	0.75
212	Reginato et al. 2008	Curitiba	PR	plot/floristic	49W 13'	25S 25'	60/70	656	0.2
213	Gris 2012*	Santa Terezinha do Itaipu	PR	plot	54W 21'	25S 27'	41	267	0.36
214	Cervi et al. 2009	Morretes	PR	floristic	48W 46'	25S 28'	138	-	-
215	Koehler et al. 2002	Morretes	PR	plot	48W 57'	25S 28'	27	-	0.05
216	Reginato & Goldenberg 2007	Piraquara	PR	plot	48W 58'	25S 28'	77	617	0.28
217	Viani et al. 2011*	Quedas do Iguaçu	PR	pc-quarter	52W 49'	25S 28'	65	704	0.5
218	Viani et al. 2011*	Quedas do Iguaçu	PR	pc-quarter	52W 52'	25S 28'	59	698	0.52
219	Gris 2012*	Santa Terezinha do Itaipu	PR	plot	54W 21'	25S 28'	65	446	0.36
220	Gris 2012*	Santa Terezinha do Itaipu	PR	plot	54W 21'	25S 28'	49	398	0.36
221	Silva et al. 1993	Paranaguá	PR	plot	48W 20'	25S 30'	77	-	0.56
222	Guapyassú 1994	Morretes	PR	plot	48W 49'	25S 30'	56	534	0.38

223	Silva 1994*	Morretes	PR	pc-quarter	48W 54'	25S 30'	73	320	0.13
224	Galvão et al. 2002	Morretes	PR	plot	48W 48'	25S 31'	12	417	0.26
225	Koehler et al. 2002	Piraquara	PR	plot	48W 55'	25S 31'	25	-	0.05
226	Gris 2012*	Santa Terezinha do Itaipu	PR	plot	54W 16'	25S 31'	54	443	0.36
227	Gris 2012*	Santa Terezinha do Itaipu	PR	plot	54W 19'	25S 31'	61	325	0.36
228	Viani et al. 2011*	Quedas do Iguaçu	PR	pc-quarter	52W 58'	25S 33'	73	752	0.61
229	Galvão et al. 2002	Pontal do Paraná	PR	plot	48W 22'	25S 34'	19	349	0.2
230	Rotta et al. 1997*	Paranaguá	PR	plot	48W 31'	25S 34'	34	556	0.28
231	Pasdiora 2003 / Iurk 2008	Araucária	PR	plot	49W 24'	25S 34'	47	602	0.2
232	Iurk 2008	Balsa Nova	PR	floristic	49W 37'	25S 34'	21	-	-
233	Blum 2006	Morretes	PR	plot	48W 42'	25S 36'	93	605	0.6
234	Scheer et al. 2011*	Morretes	PR	plot	49W 30'	25S 36'	28	557	0.12
235	Iurk 2008	Palmeira	PR	plot/floristic	50W 01'	25S 36'	35/53	1165	2.5
236	Blum 2006	Morretes	PR	plot	48W 41'	25S 37'	63	990	0.4
237	Koehler et al. 2002	Tijucas do Sul	PR	plot	49W 01'	25S 40'	19	-	0.05
238	Scheer et al. 2011*	Morretes	PR	plot	48W 47'	25S 41'	35	413	0.12
239	Galvão et al. 2002	Guaratuba	PR	plot	48W 34'	25S 43'	22	386	0.3
240	Sonehara 2005	Matinhos	PR	plot/floristic	48W 34'	25S 45'	35/70	512	0.1
241	Galvão et al. 2002	Matinhos	PR	plot	48W 33'	25S 46'	29	316	0.2

242	Galvão et al. 2002	Matinhos	PR	plot	48W 34'	25S 49'	23	439	0.32
243	Iurk 2008	São Mateus do Sul	PR	floristic	50W 22'	25S 52'	38	-	-
244	Britez et al. 1995	São Mateus do Sul	PR	floristic	50W 22'	25S 52'	131	-	-
245	Koehler et al. 2002	Tijucas do Sul	PR	plot	48W 55'	25S 54'	17	-	0.05
246	Galvão et al. 2002	Guaratuba	PR	plot	48W 46'	25S 55'	59	386	0.4
247	Negrelle 2006*	Itapoá	SC	plot	48W 37'	26S 04'	119	1955	1
248	Carvalho 2000	Joinville	SC	pc-quarter	48W 49'	26S 18'	38	276	0.64
249	Valerio et al. 2008	Clevelândia	PR	plot	52W 13'	26S 19'	26	232	0.8
250	Iza 2002*	Ilhota	SC	plot	48W 57'	26S 46'	135	1163	1
251	Negrelle & Silva 1992*	Caçador	SC	plot/floristic	51W 01'	26S 46'	43/52	276	-
252	Floss 2011*	Ponte Serrada	SC	plot	51W 58'	26S 49'	57	2935	1.56
253	Santos et al. 2012	Faxinal dos Guedes	SC	plot	52W 16'	26S 52'	36	439	0.8
254	Floss 2011*	Saudades	SC	plot	53W 01'	26S 52'	84	2159	1.56
255	Teo et al. 2012*	Lebon Régis	SC	plot	50W 40'	26S 55'	51	1699	1
256	Siminiski et al. 2004	S. P. Alcântara	SC	plot	48W 48'	27S 00'	44	850	0.6
257	Schorn & Galvão 2009*	Blumenau	SC	plot	49W 01'	27S 01'	79	1556	1.2
258	Caglioni 2013*	Blumenau	SC	plot	49W 04'	27S 01'	108	749	0.33
259	Schorn 2005*	Blumenau	SC	plot	49W 04'	27S 03'	80	785	0.4
260	Floss 2011*	Guatambu	SC	plot	52W 46'	27S 06'	74	2047	1.56

261	Ruschel et al. 2009	São Pedro de Alcântara	SC	plot	48W 48'	27S 33'	69	-	1.5
262	Higuchi et al. 2012	Campos Novos	SC	plot	51W 09'	27S 34'	86	-	1
263	Klauberg et al. 2010*	Lages	SC	plot	50W 21'	27S 46'	45	729	0.64
264	Higuchi et al. 2012	Lages	SC	plot	50W 10'	27S 51'	92	-	1
265	Martins Ramos et al. 2011	Urupema	SC	floristic	49W 55'	27S 52'	58	-	-
266	Higuchi et al. 2012	Painel	SC	plot	49W 55'	27S 55'	51	-	1
267	Santos 2003*	Siderópolis	SC	plot	49W 22'	28S 34'	77	945	0.5
268	Martins 2005*	Siderópolis	SC	plot	49W 24'	28S 34'	108	1400	1
269	Santos 2003*	Siderópolis	SC	plot	49W 24'	28S 34'	85	727	0.5
270	Pasetto 2008*	Siderópolis	SC	plot/floristic	49W 31'	28S 34'	98/141	1423	1
271	Colonetti 2008*	Siderópolis	SC	plot	49W 33'	28S 36'	105	1712	1
272	Oliveira 2008	Morro da Fumaça	SC	pc-quarter	49W 21'	28S 37'	48	193	0.12
273	Unesc 2009*	Criciúma	SC	pc-quarter	49W 21'	28S 40'	84	400	-
274	Mauhs 2002	Vacaria	RS	plot/floristic	50W 55'	28S 40'	24/58	133	0.2
275	Bosa 2011*	Morro Grande	SC	pc-quarter	49W 45'	28S 43'	95	1017	0.5
276	Martins 2010*	Timbé do Sul	SC	plot	49W 49'	28S 43'	142	3148	1
277	Silva 2006*	Criciúma	SC	plot	49W 25'	28S 48'	132	1401	1
278	Martins 2010*	Araranguá	SC	plot	49W 31'	29S 01'	26	2034	1
279	Souza 2012	Passo de Torres	SC	pc-quarter	49W 43'	29S 13'	66	-	-

280	Santos et al. 2012	Torres	RS	plot	49W 45'	29S 19'	76	4060	0.25
281	Sonego et al. 2007*	São Francisco de Paula	RS	plot	50W 22'	29S 22'	40	417	0.29
282	Rossoni & Baptista 1995	Arroio do Sal	RS	floristic	49W 50'	29S 28'	70	-	-
283	Jarenkow & Waechter 2001*	Vale do Sol	RS	plot	52W 40'	29S 34'	55	1855	1
284	Oliveira et al. 2005	Porto Alegre	RS	floristic	50W 43'	29S 49'	52	-	-
285	Oliveira et al. 2005	Porto Alegre	RS	floristic	50W 46'	29S 49'	36	-	-
286	Oliveira et al. 2005	Porto Alegre	RS	floristic	50W 48'	29S 49'	75	-	-
287	Oliveira et al. 2005	Porto Alegre	RS	floristic	50W 51'	29S 49'	40	-	-
288	Oliveira et al. 2005	Porto Alegre	RS	floristic	50W 30'	29S 55'	56	-	-
289	Oliveira et al. 2005	Porto Alegre	RS	floristic	50W 36'	29S 55'	18	-	-
290	Oliveira et al. 2005	Porto Alegre	RS	floristic	50W 42'	29S 58'	50	-	-
291	Oliveira et al. 2005	Porto Alegre	RS	floristic	50W 40'	30S 01'	41	-	-
292	Waechter et al. 2000	Viamão	RS	pc-quarter	50W 49'	30S 04'	24	-	-
293	Oliveira et al. 2005	Porto Alegre	RS	floristic	50W 57'	30S 09'	25	-	-
294	Oliveira et al. 2005	Porto Alegre	RS	floristic	50W 58'	30S 09'	30	-	-
295	Moraes & Mondin 2001*	Palmares do Sul	RS	pc-quarter	50W 18'	30S 21'	31	120	-
296	Scherer et al. 2005*	Viamão	SC	plot	51W 00'	30S 22'	28	1029	1.02
297	Jurinitz & Jarenkow 2003*	Camaquã	RS	plot	51W 52'	30S 40'	69	2236	1
298	De Marchi & Jarenkow 2008*	Cristal	RS	plot	51W 55'	31S 01'	29	2179	1

299	Dorneles & Waechter 2004*	Tavares	RS	pc-quarter	50W 50'	31S 10'	21	240	-
300	Venzke & Martins 2013	Arroio do Padre	RS	plot	52W 28'	31S 25'	70	-	1.2

*Studies comprising the dataset of survey studies that evaluated a minimum of 200 individuals with diameter at breast height ≥ 5cm.

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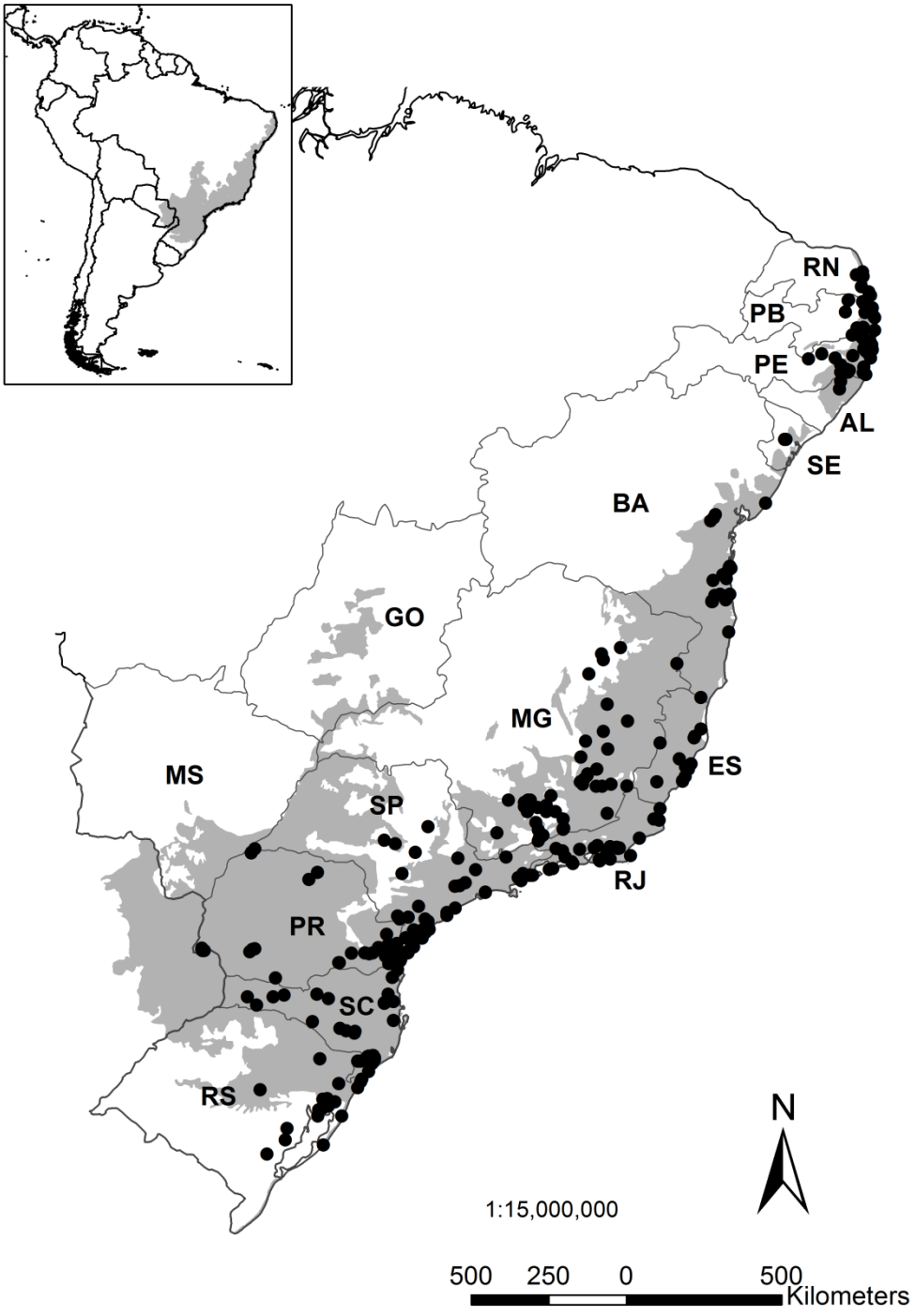
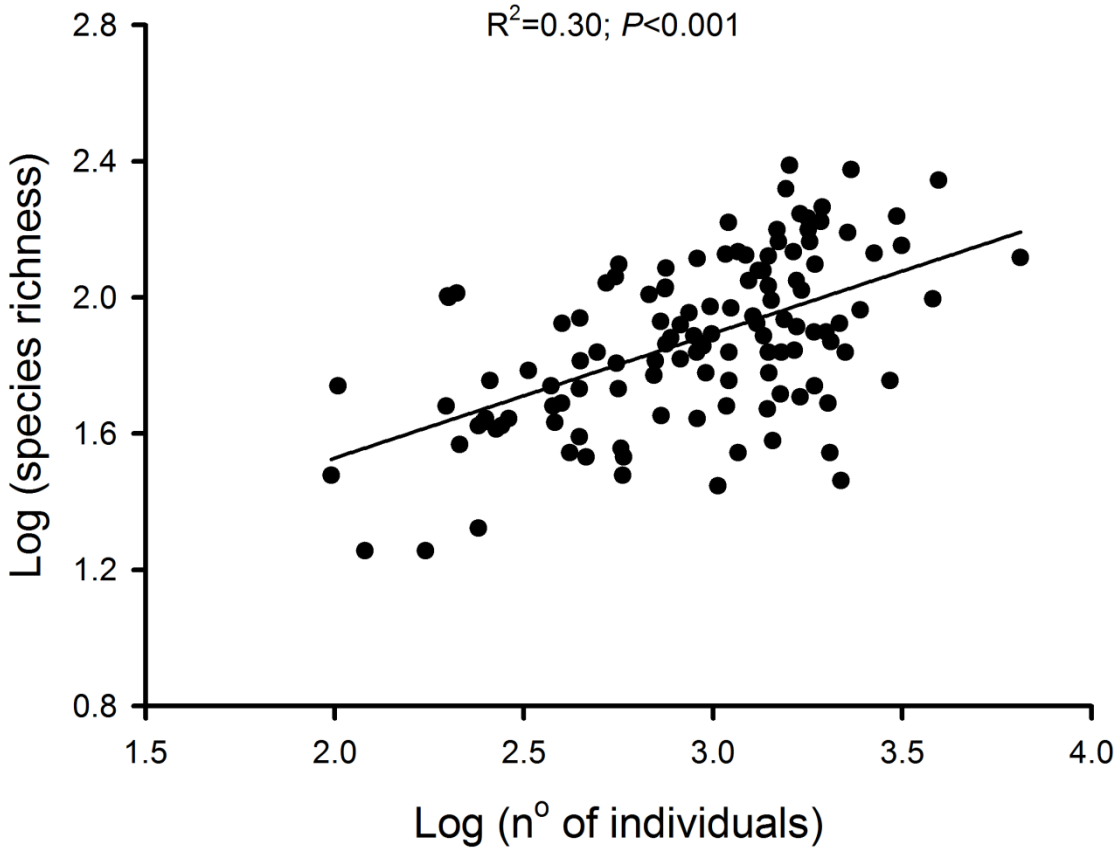
Appendix A2. Location of all compiled plant survey studies in the Atlantic Forest. Brazilian states: Rio Grande do Sul (RS); Santa Catarina (SC); Paraná (PR); São Paulo (SP); Mato Grosso do Sul (MS); Goiás (GO); Rio de Janeiro (RJ); Espírito Santo (ES); Minas Gerais (MG); Bahia (BA); Sergipe (SE); Alagoas (AL); Pernambuco (PE); Paraíba (PB); Rio Grande do Norte (RN).



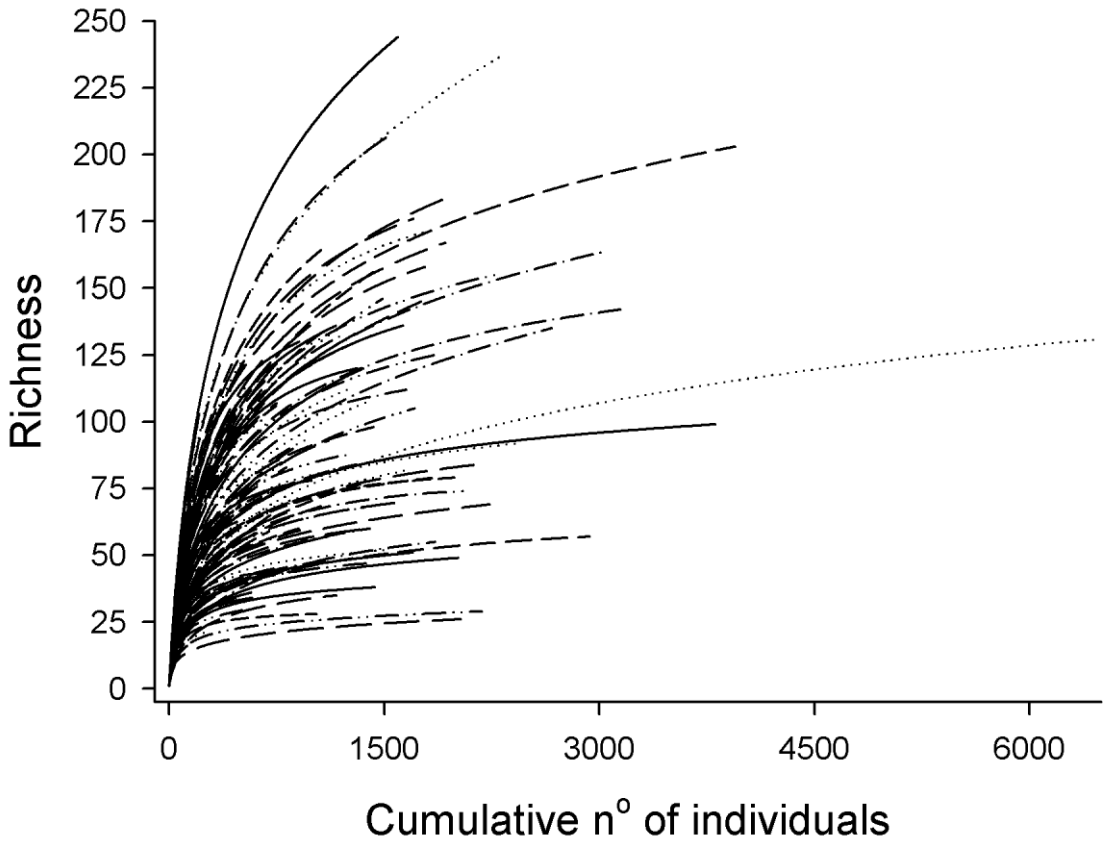
Appendix A3. Pearson's correlation of environmental predictor variables

Variable	Code	AET	BIO1	BIO2	BIO5	BIO6	BIO12	BIO13	BIO14	ALSA	ECEC	PHAQ	TAWC
Actual evapotranspiration	AET	-	-	-	-	-	-	-	-	-	-	-	-
Annual mean temperature	BIO1	-0.37	-	-	-	-	-	-	-	-	-	-	-
Mean diurnal range	BIO2	0.23	-0.50	-	-	-	-	-	-	-	-	-	-
Max. temperature of warmest month	BIO5	-0.16	0.83	-0.16	-	-	-	-	-	-	-	-	-
Min. temperature of coldest month	BIO6	-0.45	0.95	-0.69	0.66	-	-	-	-	-	-	-	-
Annual precipitation	BIO12	0.81	-0.25	-0.12	-0.23	-0.23	-	-	-	-	-	-	-
Precipitation of wettest month	BIO13	0.52	-0.04	0.11	-0.14	-0.10	0.70	-	-	-	-	-	-
Precipitation of driest month	BIO14	0.54	-0.39	-0.23	-0.23	-0.30	0.56	-0.15	-	-	-	-	-
Soil exchangeable aluminum percentage	ALSA	0.20	-0.07	-0.10	-0.09	-0.05	0.22	0.12	0.18	-	-	-	-
Soil effective cation exchange capacity	ECEC	0.25	-0.40	0.16	-0.30	-0.38	0.19	0.11	0.20	-0.13	-	-	-
Soil pH measured in water	PHAQ	-0.14	0.09	-0.01	0.16	0.06	-0.12	-0.05	-0.11	-0.55	0.15	-	-
Soil available water capacity	TAWC	0.20	-0.31	-0.02	-0.22	-0.29	0.22	0.09	0.24	0.30	0.72	0.01	-
Total organic carbon content	TOTC	0.35	-0.51	0.20	-0.42	-0.48	0.28	0.11	0.34	0.16	0.81	-0.25	0.65

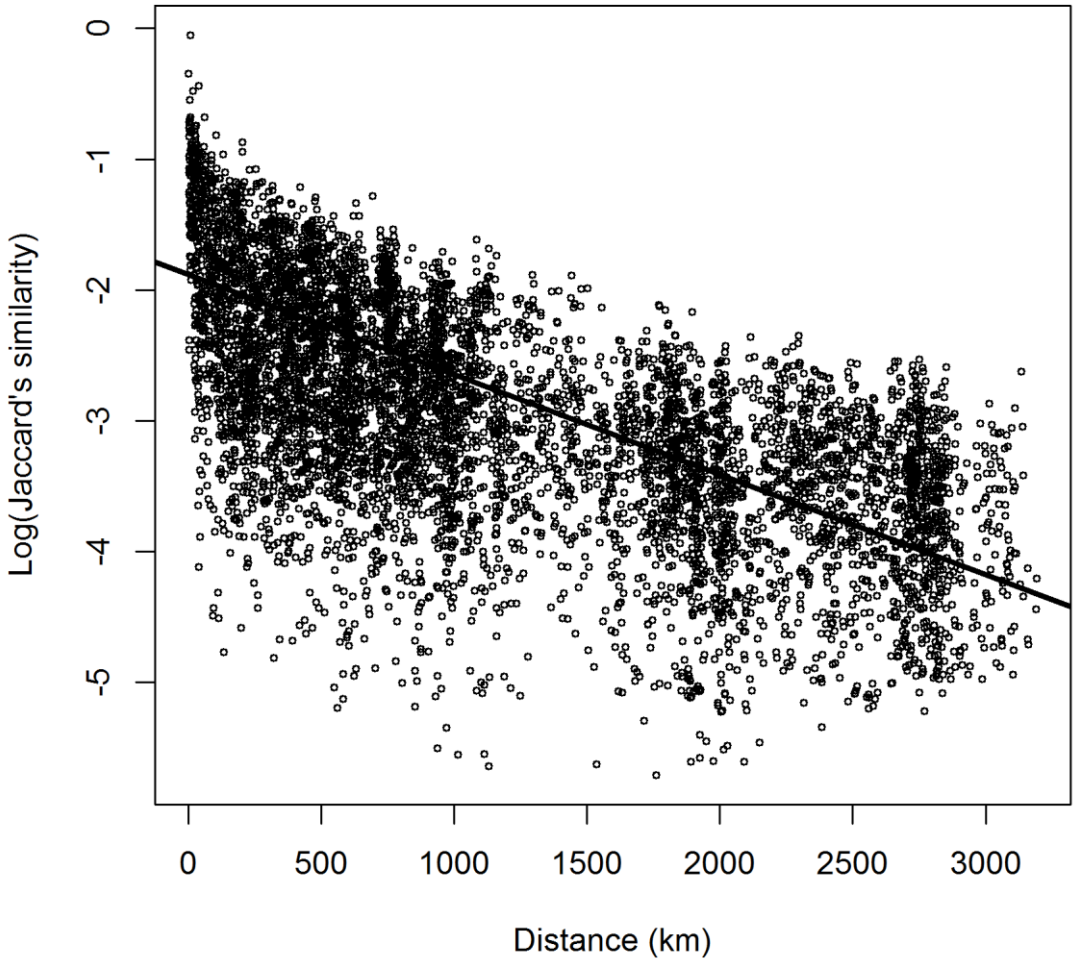
Appendix A4. Linear regression of number of individuals vs. species richness for the compiled survey studies that evaluated individuals with diameter at breast height ≥ 5cm. Slope=0.36; intercept=0.80



Appendix A5. Species accumulation curves from quantitative plant survey studies in the Atlantic Forest. The extrapolation/rarefaction of the number of species was based on 1200 sample individuals and the Chao1 estimator (Colwell *et al*., 2012). The'target' richness was chosen according to the average number of sample individuals obtained from the compiled survey studies that evaluated a minimum of 200 individuals with diameter at breast height ≥ 5cm. Each line represents a survey study.



Appendix A6. Regression of pairwise similarity in species composition against geographical distance. We applied generalized linear models (GLM) with a log-link function. This approach also models the logarithm of similarity values as a linear function of distance, but does not require an explicit log-transformation of the observed similarity values. Distance-decay measured as the distance at which 50% of the maximum similarity is observed was 376 km.



6.2 Capítulo 2

Table S1. Comparisons of representation of each feature between the biodiversity scenario (only species were considered for prioritization) and all-dimensions scenario (species and socioeconomic features) within top priority sites for different management scenarios and conservation targets in the Atlantic Forest. Values represent the difference (loss is negative, gain is positive) in feature representation achieved by the all-dimensions scenario under low greenhouse gas emission scenarios in 2050.

Features	Conservation only*			Conservation prior to restoration			Unconstrained		
	10%	17%	20%	10%	17%	20%	10%	17%	20%
Biodiversity	-8.93	-	-	-0.79	-0.43	-0.91	-0.58	-2.02	-2.73
Land-use	-15.43	-	-	-5.50	-1.84	-3.52	-5.44	-9.73	-10.82
Political-willingness	5.84	-	-	-0.08	3.25	4.47	3.20	7.50	8.52
Land cost	-56.11	-	-	-33.54	-1.83	-3.71	-29.01	-37.49	-41.65

*comparisons restricted to current forest remnants; comparisons of 17% and 20% top priority sites are not possible for the ‘conservation only’ management scenario, given that only 12% of the Atlantic Forest original extent is available for conservation

Table S2. Comparisons of representation of each feature between the biodiversity scenario (only species were considered for prioritization) and all-dimensions scenario (species and socioeconomic features) within top priority sites for different management scenario and conservation targets in the Atlantic Forest. Values represent the difference (loss is negative, gain is positive) in feature representation achieved by the all-dimensions scenario under high greenhouse gas emission scenarios in 2050.

Features	Conservation only*			Conservation prior to restoration			Unconstrained		
	10%	17%	20%	10%	17%	20%	10%	17%	20%
Biodiversity	-8.59	-	-	-0.80	-0.39	-0.91	-0.59	-2.19	-2.99
Land-use	-11.07	-	-	-3.35	-1.54	-2.99	-3.87	-7.29	-8.13
Political-willingness	6.79	-	-	0.81	2.95	4.54	3.36	9.12	11.32
Land cost	-55.53	-	-	-33.26	-2.00	-4.59	-29.04	-36.98	-40.78

*comparisons restricted to current forest remnants; comparisons of 17% and 20% top priority sites are not possible for the ‘conservation only’ management scenario, given that only 12% of the Atlantic Forest original extent is available for conservation

Table S3. Pearson correlations between rankings of top priority sites for different management and greenhouse gas emission scenarios in the Atlantic Forest projected for the year of 2050.

Emission scenario/conservation target	Conservation only*	Conservation prior to restoration	Unconstrained
Low emission vs. high emission / 10%	0.99	0.99	0.89
Low emission vs. high emission / 17%	-	0.99	0.61
Low emission vs. high emission / 20%	-	0.95	0.60
High emission vs. low emission / 10%	0.99	0.99	0.91
High emission vs. low emission / 17%	-	0.99	0.72
High emission vs. low emission / 20%	-	0.99	0.73

*comparisons restricted to current forest remnants; comparisons of 17% and 20% top priority sites are not possible for the 'conservation only' management scenario, given that only 12% of the Atlantic Forest original extent is available for conservation

Table S4. Pearson correlations between rankings of top priority sites in the management scenario of conservation of forest remnants prior to restoration of degraded habitat ('conservation prior to restoration') and no *a priori* definition of action ('unconstrained') for different conservation targets and climate scenarios in the Atlantic Forest projected for the year of 2050.

Management scenario/conservation target	Low emission	High emission
Conservation prior to restoration vs. unconstrained / 10%	0.59	0.58
Conservation prior to restoration vs. unconstrained / 17%	0.50	0.49
Conservation prior to restoration vs. unconstrained / 20%	0.29	0.28
Unconstrained vs. conservation prior to restoration / 10%	0.89	0.90
Unconstrained vs. conservation prior to restoration / 17%	0.89	0.88
Unconstrained vs. conservation prior to restoration / 20%	0.88	0.87

Table S5. Number of species and average proportion of species distribution remaining, in parenthesis, within top priority areas for different management scenarios. Comparisons are shown for priority areas within current protected areas (PAs) and for different conservation targets in the Atlantic Forest under low and high greenhouse gas emission scenarios in 2070.

Management scenario	Low emission				High emission			
	PAs	10%	17%	20%	PAs	10%	17%	20%
Conservation only*	2218 (0.37)	2253 (0.85)	-	-	2221 (0.37)	2253 (0.85)	-	-
Conservation prior to restoration	2252 (0.09)	2254 (0.15)	2254(0.26)	2254 (0.32)	2251 (0.09)	2254 (0.15)	2254(0.26)	2254 (0.32)
Unconstrained	2252 (0.09)	2254 (0.17)	2254(0.30)	2254 (0.34)	2251 (0.09)	2253 (0.17)	2254(0.30)	2254 (0.34)

*comparisons restricted to current forest remnants; comparisons of 17% and 20% top priority sites are not possible for the ‘conservation only’ management scenario, given that only 12% of the Atlantic Forest original extent is available for conservation

Table S6. Comparisons of representation of each feature between the biodiversity scenario (only species were considered for prioritization) and all-dimensions scenario (species and socioeconomic features) within top priority sites for different management scenario and conservation targets in the Atlantic Forest. Values represent the difference (loss is negative, gain is positive) in feature representation achieved by the all-dimensions scenario under low greenhouse gas emission scenarios in 2070.

Features	Conservation only*			Conservation prior to restoration			Unconstrained		
	10%	17%	20%	10%	17%	20%	10%	17%	20%
Biodiversity	-9	-	-	-0.82	-0.43	-0.91	-0.60	-2.05	-2.76
Land-use	-15.22	-	-	-5.52	-1.85	-3.50	-5.57	-9.57	-10.65
Political-willingness	5.97	-	-	-0.06	3.24	4.54	2.90	7.96	9.02
Land cost	-56.05	-	-	-33.45	-1.87	-3.84	-29.08	-37.67	-41.40

*comparisons restricted to current forest remnants; comparisons of 17% and 20% top priority sites are not possible for the ‘conservation only’ management scenario, given that only 12% of the Atlantic Forest original extent is available for conservation

Table S7. Comparisons of representation of each feature between the biodiversity scenario (only species were considered for prioritization) and all-dimensions scenario (species and socioeconomic features) within top priority sites for different management scenarios and conservation targets in the Atlantic Forest. Values represent the difference (loss is negative, gain is positive) in feature representation achieved by the all-dimensions scenario under high greenhouse gas emission scenarios in 2070.

Features	Conservation only*			Conservation prior to restoration			Unconstrained		
	10%	17%	20%	10%	17%	20%	10%	17%	20%
Biodiversity	-8.66	-	-	-0.77	-0.44	-1.12	-0.62	-2.23	-3.07
Land-use	-10.64	-	-	-3.23	-1.72	-3.00	-3.83	-7.12	-7.93
Political-willingness	7.24	-	-	-0.35	3.02	5.57	3.30	9.58	12.15
Land cost	-55.55	-	-	-33.58	-2.07	-4.41	-29.40	-36.78	-41.05

*comparisons restricted to current forest remnants; comparisons of 17% and 20% top priority sites are not possible for the ‘conservation only’ management scenario, given that only 12% of the Atlantic Forest original extent is available for conservation

Table S8. Comparisons of representation of each feature between the management scenario of conservation of forest remnants prior to restoration of degraded habitat ('conservation prior to restoration') and no *a priori* definition of action ('unconstrained') within top priority sites for different conservation targets in the Atlantic Forest. Values represent the difference (loss is negative, gain is positive) in feature representation achieved by the conservation prior to restoration scenario under low and high greenhouse gas emission scenarios in 2070.

Features	Low emission			High emission		
	10%	17%	20%	10%	17%	20%
Biodiversity	-1.70	-3.95	-2.72	-1.56	-3.51	-2.31
Land-use	0.82	6.84	6.51	0.89	3.93	3.61
Political-willingness	-1.43	-2.47	-3.06	-1.44	-4.85	-5.56
Land cost	1.91	36.60	36.32	1.91	36.17	35.60

Fig. S9

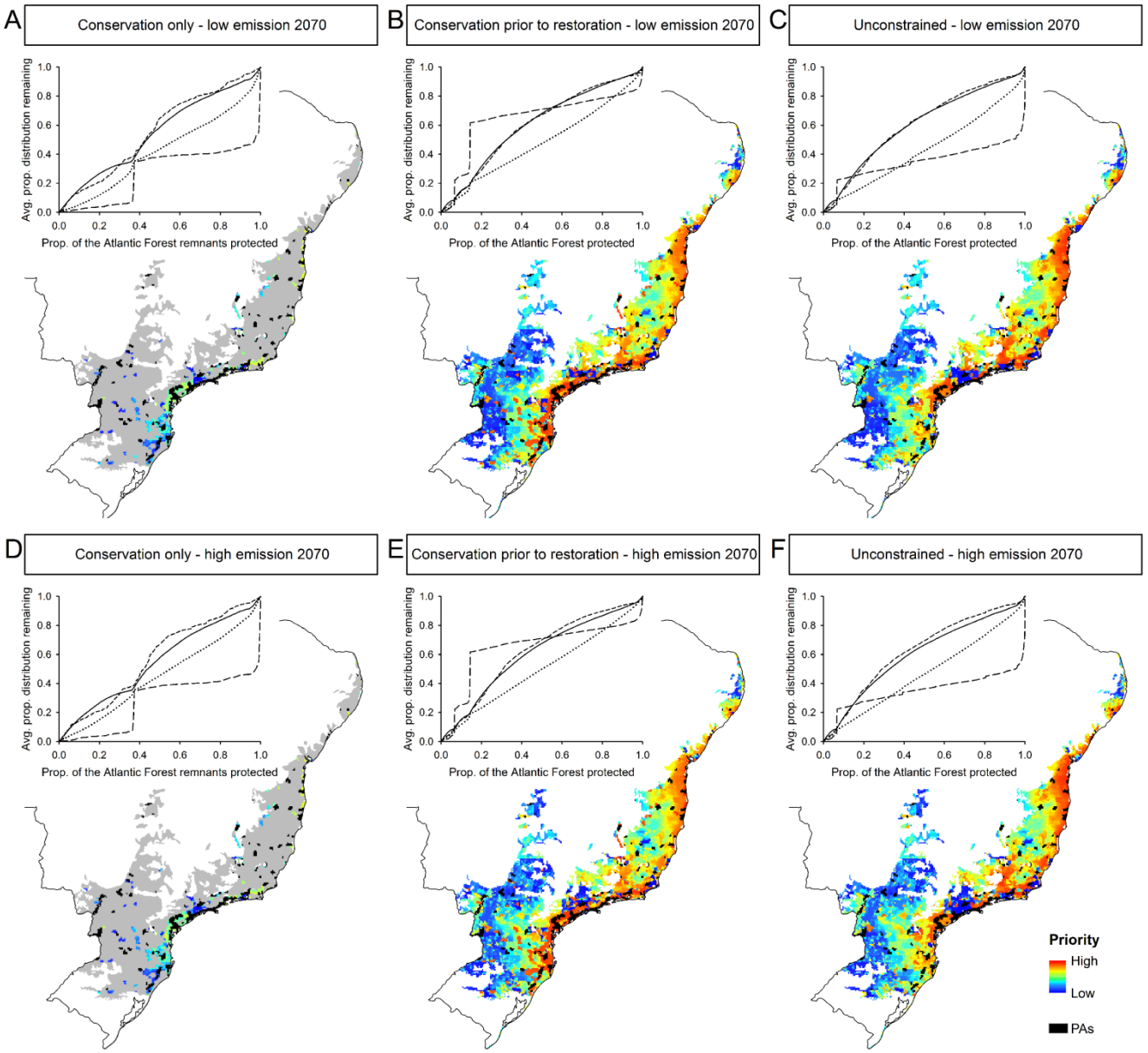
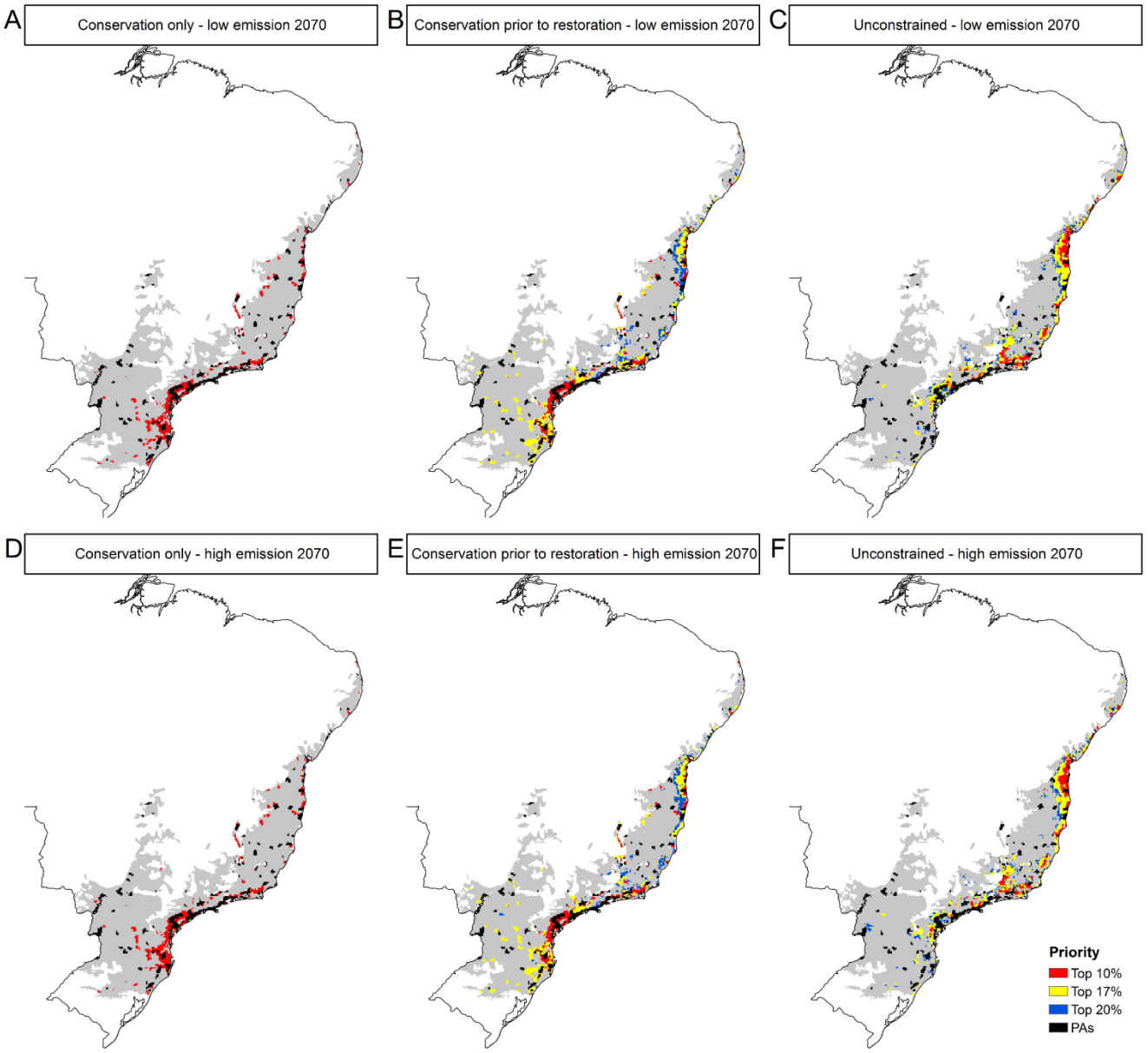

A
Conservation only - low emission 2070
B
Conservation prior to restoration - low emission 2070
C
Unconstrained - low emission 2070
D
Conservation only - high emission 2070
E
Conservation prior to restoration - high emission 2070
F
Unconstrained - high emission 2070
Avg. prop. distribution remaining
Prop. of the Atlantic Forest remnants protected
Prop. of the Atlantic Forest protected
Priority
High
Low
PAs

Fig. S10


A
Conservation only - low emission 2070
B
Conservation prior to restoration - low emission 2070
C
Unconstrained - low emission 2070
D
Conservation only - high emission 2070
E
Conservation prior to restoration - high emission 2070
F
Unconstrained - high emission 2070
Priority
Top 10%
Top 17%
Top 20%
PAs